The Journal of ARACHNOLOGY

OFFICIAL ORGAN OF THE AMERICAN ARACHNOLOGICAL SOCIETY

VOLUME 33 2005 NUMBER 3

The Journal of Arachnology (ISSN 0161-8202), a publication devoted to the study of Arachnida, is published three times each year by *The American Arachnological Society*. **Memberships (yearly):** Membership is open to all those interested in Arachnida. Subscriptions to *The Journal of Arachnology* and *American Arachnology* (the newsletter), and annual meeting notices, are included with membership in the Society. Regular, $40; Students, $25; Institutional, $125 . Inquiries should be directed to the Membership Secretary (see below). **Back Issues:** Patricia Miller, P.O. Box 5354, Northwest Mississippi Community College, Senatobia, Mississippi 38668 USA. Telephone: (601) 562-3382. **Undelivered Issues:** Allen Press, Inc., 1041 New Hampshire Street, P.O. Box 368, Lawrence, Kansas 66044 USA.

Cover photo: The pseudoscorpion *Saetigerocreagris setifera*. Photo by Rick Vetter.

Publication date: 28 December 2005

♾ **This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).**

2005. The Journal of Arachnology 33:641–662

THE MALE GENITALIA OF THE FAMILY ATEMNIDAE (PSEUDOSCORPIONES)

Finn Erik Klausen: Department of Natural Sciences, Agder University College, Servicebox 422, N-4604 Kristiansand, Norway. E-mail: finn.e.klausen@hia.no

ABSTRACT. Knowledge of the male genitalia of the Atemnidae is still limited, although several authors have previously contributed to our understanding of their structure. This study deals with the morphology and configuration of the male genital organs. Forty-four species belonging to 16 different genera have been investigated, including species of 4 genera of Miratemninae. *Anatemnus longus* Beier 1932 is synonymized with *A. voeltzkowi* (Ellingsen 1908), *Paratemnoides ceylonicus* (Beier 1932) is synonymized with *P. pallidus* (Balzan 1892), and *P. minor* (Balzan 1892) with *P. nidificator* (Balzan 1888). *Tamenus equestroides* (Ellingsen 1906) is moved to the genus *Cyclatemnus*. The genitalia of the investigated specimens are described and a general diagnostic description of the male genitalia of the family is given. The study reveals an overall uniformity in the genitalic configuration of the family, which indicates monophyly. With respect to the affinities with other families of the Cheliferoidea, the male genitalia suggest that the Atemnidae might be closer to the Withiidae than to the Cheliferidae or Chernetidae. Claimed differences between the Atemninae and Miratemninae are considered, but the morphology of the male genitalia does not support their division into two families. Comparison of species of the genera *Anatemnus*, *Catatemnus*, *Oratemnus* and *Paratemnoides* reveals greater variation within the genera than between different genera. This infers that the present systematic grouping of species does not reflect true phylogenetic relationships within the family.

Keywords: Arachnida, pseudoscorpion, genitalia, morphology, phylogenetic relationships

The male genitalia of pseudoscorpions are used for indirect sperm insertion, the male produces a spermatophore with a sperm packet on a stalk which is deposited on the substratum. The female is later inseminated from the sperm in this spermatophore. Accordingly the male has no copulatory organ, but the whole of the male genitalia is internally situated with the opening located between the second and third sternite of the abdomen. The spermatophore is produced in the chitinized genital chamber with its diverticula and associated glands. The genitalia can have a complex structure, which to a certain degree is reflected in a correspondingly complex structure of the spermatophore. The complex structure of the genitalia is perhaps most pronounced in the Cheliferoidea which includes the family Atemnidae, and may have potential in systematic work.

Several authors have dealt with the morphology of the male genitalia of species in the family Atemnidae, most extensively Vachon (1938a); but others have contributed, notably Chamberlin (1931, 1939, 1947), Dashdamirov and Schawaller (1993), Dumitresco and Orghidan (1969), Heurtault (1970) and Harvey (1988).

The complex structure and the internal location makes the genitalia difficult to examine in situ, this may be part of the reason why the knowledge of the morphology is still rather limited and has been used very little for diagnostic characters in the description of genera and species. However, an early attempt to discriminate taxonomically between different species in the genera *Catatemnus* Beier 1932, *Cyclatemnus* Beier 1932 and *Tamenus* Beier 1932 was made by Vachon (1938b).

Traditionally the delimitation of the family Atemnidae and the diagnoses of the different genera in the family was thus based on external characters. The family was erected by Chamberlin (1931) and subdivided into several genera by Beier (1932a, 1932b). Beier further divided the family into two subfamilies, Atemninae and Miratemninae. The Miratemninae was elevated to full family level, Miratemnidae by Dumitresco and Orghidan (1970), partly based on their investigation on the male genitalia of *Diplotemnus insolitus* Chamberlin 1933 and its difference in orien-

tation compared to the Atemninae. But Harvey (1991, 1992) did not accept the family status of the miratemnids. He argued against it and returned them to the family Atemnidae.

The subfamily Atemninae comprises genera which have a problematic taxonomic position. The delimitations of the genera are based on external characters which on several occasions appear to be continuous and thus of less diagnostic value. This implies that the present delimitations of the genera probably do not reveal the true relationship between them. In this context, it might be valuable to make a broader survey of male genitalia both of the Miratemninae and the Atemninae, in an attempt to use these organs in the delimitation of monophyletic taxa.

METHODS

This investigation is based on the examination of male genital organs from the following 44 species representing 16 of the 19 extant genera, including species of four genera of Miratemninae. The nomenclature follows the catalogue of Harvey (1991).

Abbreviations.—AUC = Agder University College, Norway; BPBM = Bernice P. Bishop Museum, Honolulu; CAS = California Academy of Sciences, San Francisco; MHNG = Muséum d'Histoire naturelle, Geneva; NHMW = Naturhistorisches Museum, Wien; NMP = Natal Museum, Pietermaritzburg; NRMS = Naturhistoriska Riksmuséet, Stockholm; RMCA = Royal Museum of Central Africa, Tervuren; SMNS = Staatliches Museum für Naturkunde, Stuttgart; TMP = Transvaal Museum, Pretoria; WAM = Western Australian Museum, Perth; ZMB = Museum für Naturkunde, Humboldt-Universität, Berlin; ZMUO = Zoological Museum, University of Oslo.

Family Atemnidae Chamberlin 1930
Subfamily Miratemninae Beier 1932

Brazilatemnus browni Muchmore 1975

Material examined.—BRAZIL: Pará, Porto Trompetas, August 1992, J.D. Majer leg. (WAM; Harvey det.).

Diplotemnus insolitus Chamberlin 1933

Material examined.—SPAIN: Gran Canaria, Maspalomas, dunes, 16 March 1994, C. Wurst leg. (SMNS, no. 3448; Schawaller det.).

Miratemnus hirsutus Beier 1955

Material examined.—SOUTH AFFRICA: Pretoria,1958 (RMCA; Beier det.); Cape Province, Cape Houtbaai, December 1960 (TMP, no. ZA 46; Klausen det.); E.Cape, Grahamstown, Harpers Hall, October 1943, W. G. Rump leg. (NMP, no. 668). RHODESIA (ZIMBABWE): Inyanda, February 1969, R. Mussard leg. (MHNG; Beier det.).

Miratemnus kenyaensis Mahnert 1983

Material examined.—KENYA: Namanga, 21 March 69, Å. Holm leg. (MHNG; paratype); Lake Elmenteita, 1800 m, SS. pierres (under stones?), 7 November 1977, Mahnert & Perret leg. (MHNG; paratype).

Miratemnus zuluanus Lawrence 1937

Material examined.—SOUTH AFRICA: KZN, Drummond, February 1942, W.G. Rump leg. (NMP, no. 661; Beier det.).

Tullgrenius indicus Chamberlin 1933

Material examined.—INDIA: Tamil Nadu; Amman Nagar, N.of Coimbatore, 6 December 2000, F. Klausen leg. (AUC; Klausen det.)

Subfamily Atemninae Chamberlin 1930

Anatemnus angustus (Redikorzev 1938)

Material examined.—VIETNAM: Plateau Lang Biang (= Cao Nguyên Lâm Viên), 1938–39, C. Dawydoff leg. (NHMW; Beier det.).

As *Oratemnus indicus*: INDIA: Mysore, 12 mil. E of Virajpet, 24 February 1962, Ross & Cavagnaro leg. (CAS; Beier det.).

As *Anatemnus nilgiricus*: INDIA: Mysore, 8 mi. NE Mercara, 1000 m, 22 February 1962, E. S. Ross & D. Q. Cavagnaro leg. (CAS; Beier det.).

Remarks.—The specimens identified as *O. indicus* and *A. nilgiricus* are, as far as I can judge, both in configuration of the genitalia and in outer morphology identical to *A. angustus*. The specimens of *O. indicus* have been compared with the holotype of *Chelifer indicus* deposited in Zoological Museum in Copenhagen and the description given by With (1906). The dorsal tubercle of the trochanter of the holotype is blunt ended and not pointed as in the specimens in my custody. I have not been able to compare the specimen identified as *A. nilgiricus* with the type ma-

terial in the Roewer collection. However, in the description given by Beier (1932a) of *A. nilgiricus*, he states that the dorsal tubercle of the trochanter is blunt ended or rounded, contrary to the specimen above which has a conical and pointed dorsal tubercle.

The genitalia of *A. angustus* are identical with those of the syntype of *Catatemnus birmanicus* from Naturhistoriska Riksmuséet, Stockholm. Moreover, apart from the appearance of the carapace of *C. birmanicus* they are similar in external morphology. That is, the shape of the trochanter and patella of the pedipalps are similar, the trichobothria of the fingers have the same configuration and so have the tergal seta of the abdomen.

Anatemnus elongatus (Ellingsen 1902)

Material examined.—ECUADOR: As *Chelifer* (*Atemnus*) *elongatus*: by Guayaquil, June 1901, Ortoneda leg. (ZMUO, no.102; syntype)

Anatemnus javanus (Thorell 1883)

Material examined.—PAPUA NEW GUINEA: As *Chelifer* (*Atemnus*) *javanus*: Bismarck Archipelago, Fr. Dahl leg. (ZMUO, no. 319; Ellingsen det.).

Anatemnus novaguineensis (With 1908)

Material examined.—PAPUA NEW GUINEA: Finschhafen, 17 April 1944, E. S. Ross leg. (CAS; Beier det.).

Anatemnus orites (Thorell 1889)

Material examined.—As *Chelifer* (= *Anatemnus*) *orites*: BURMA (MYANMAR): Thenasserim, Plapoo, Fea leg. (NRMS, no. 6; Coll.[ection of?] Thorell); [Probably Carin Ghecu, Tao, 13–1400 m,1885–1887], Fea leg. (ZMUO, no. 566; Ellingsen det.).

As *Chelifer* (= *Oratemnus*) *indicus*: INDIA: Gravely, 1912 (ZMUO, no. 593; Ellingsen [?] det.).

Remarks.—The specimens identified as *A. orites* have been compared with syntypes of *Chelifer orites* from Zoological Museum in Copehagen. They are identical in outer morphology, and so is the specimen identified as *Chelifer indicus* which has been compared with the holotype of *C. indicus*. The only divergence is the form of the conical dorsal tubercle of the trochanter which is slightly higher in the holotype of *C. indicus*.

The genitalia of *A. orites* are very similar to those of *A. angustus*. With respect to the characters of the outer morphology they are similar except for the conical dorsal tubercle of the trochanter which is blunt ended in *A. orites* and pointed in *A. angustus*.

Anatemnus subvermiformis
Redikorzev 1938

Material examined.—VIETNAM: Plateau Lang Biang [= Cao Nguyên Lâm Viên], 1938–39, C. Dawydoff leg. (NHMW; Beier det.).

Anatemnus voeltzkowi (Ellingsen 1908)

Chelifer (*Atemnus*) *voeltzkowi elongata* Ellingsen 1908: 488 (junior primary homonym of *Chelifer* (*Atemnus*) *elongatus* Ellingsen, 1902).

Anatemnus longus Beier 1932: 586 (replacement name for Chelifer (Atemnus) voeltzkowi elongata Ellingsen 1908). NEW SYNONYMY.

Material examined.—As *Chelifer* (*Atemnus*) *voeltzkowi*: MADAGASCAR: SW Madagascar,Voeltzkow leg. (ZMUO, no. 307; syntype).

As *Chelifer* (*Atemnus*) *voeltzkowi elongata*: MADAGASCAR: Marovoay, September 1906, W. Kaudern leg. (ZMUO, no. 336; syntype).

Remarks.—The specimens of *A. voeltzkowi* and *A. longus* in ZMUO are unquestionably syntypes, the rest of the type series being deposited in the Zoological Museums in Berlin and in Stockholm. *Anatemnus longus* was originally described by Ellingsen (1908) as a variety of *A. voeltzkowi*. I can find no significant differences in external morphology between the two and the male genitalia are identical. Accordingly I consider *A. longus* as a synonym of *A. voeltzkowi*.

Atemnus politus (Simon 1878)

Material examined.—ITALY: prov. Basilicata, Lido San Basilia, comm. Metaponta, sieving in *Pinetum* near shore, 4 September 1993, V. Mahnert leg. (MHNG; Mahnert det.). SPAIN: Rincon de Ademuz, N. Puebla de San Miguel, *Quercus* forest, 22 April 1984, Schawaller leg. (SMNS, no 1057; Schawaller det.); Mallorca, Road between Poreres and Vilafranca, 5 May 2000, under stones in *Quercus ilex* forest, F. Klausen leg. (AUC; Klausen det.). TURKEY: Anatolien, Akzehir, 22 April 1960 (NHMW; Beier det.).

Atemnus syriacus (Beier 1955)

Material examined.—TURKEY: Köycegiz,17 February 1969 (NHMW; Beier det.).

Athleticatemnus pugil Beier 1979

Material examined.—As *Cyclatemnus granulatus*: BELGIAN CONGO (DEMOCRATIC REPUBLIC OF CONGO): Kivu, Terre Kalehe, Frangi, 18 August 1960, Musanola & Kangeta leg. (RMCA, no. 118.580; Beier det.).

Remarks.—Although Beier (1979) placed this genus close to *Titanatemnus* in his description of the species, the single specimen identified by me is very similar to *Cyclatemnus granulatus* in external morphology. Apart from the shallow or very blunt dorsal tubercle of the trochanter in *A. pugil* (which is pointed in *C. granulatus*) the characters are similar including the configuration of discal setae on the tergites. Admittedly, the palpal hand of *A. pugil* is very robust in the dorsoventral direction, but so is the palpal hand of *C. granulatus*, even if this is slightly less so. The male genitalia is closer to *Cyclatemnus* in appearance than to *Titanatemnus*, although it is not similar to *C. granulatus*.

Catatemnus birmanicus (Thorell 1889)

Material examined.—BURMA (MYANMAR): Bhamô (NRMS; syntype, Doria ded. [sic]).

As *Chelifer* (*Anatemnus*) *orites*: INDONESIA: Sumatra, [probably: Si-Rambé or Pangherang-Pisang, 1891/94, E. Modigliani leg.] (ZMUO, no. 539, Ellingsen det.).

Remarks.—The syntypes from Naturhistoriska Riksmuséet, Stockholm have been compared with the syntypes from Zoological Museum in Copenhagen. They are all identical in outer morphology and thus seem to be a homogenous group of syntypes.

The species (and genus) are separated from those of *Anatemnus* and *Oratemnus* by the character of the carapace, given as a transversal furrow or "Querfurche" by Beier (1932a, 1932b). As remarked under the species *A. angustus* and *A. orites*, the genitalia of these two are similar or identical to *C. birmanicus*, which seem to contradict the separation of them in different genera.

Catatemnus granulatus Mahnert 1978

Material examined.—CAMEROON: S.Kribi, Rocheur de Loup 17 February 1980, primary forest, Ferrara & Schlogal leg. (SMNS, no. 513; Mahnert det.).

As *Cyclatemnus burgeoni*: BELGIAN CONGO (DEMOCRATIC REPUBLIC OF CONGO): Ibembo, February 1952, R.F. Hutsebaut leg. (RMCA, no.72.809; Beier det.).

Catatemnus togoensis (Ellingsen 1910)

Material examined.—NIGERIA: Lagos, Iseri, 26 March 1949 [1929?]), Malkin leg. (NHMW; Beier det.). GHANA: Akumadan 2 September 1966. 350 m. E.S.Ross & K. Lorentzen leg. (CAS; Beier det.).

As *Catatemnus congicus*: BELGIAN CONGO (DEMOCRATIC REPUBLIC OF CONGO): 50 km. S.of Chela, 26 July 1957. Ross & Leech leg. (CAS; Beier det.).

As *Cyclatemnus fallax*: KENYA: Kaiomosi Mission, 27 mi. NE of Kisumu,1650 m, 29 November 1957 (CAS; Beier det.).

As *Tamenus femoratus* (in part): IVORY COAST: Divo, 16 August 1963. J. Decelle leg. (RMCA, no.161.132; Heurtault det.).

As *Chelifer* (= *Titanatemnus*) *sjoestedti*: CAMEROON: (no locality and date given),Y. Sjöstedt leg. (NRMS; Tullgren det.); Itoki, February 1891, Y. Sjöstedt leg. (NRMS; included in syntype material of *Chelifer sjoestedti*, Tullgren det.).

Remarks.—The identification of *C. togoensis* as *T. sjoestedti* is probably due to a misinterpretation of the specimens as juveniles of *T. sjoestedti*. The 4 males and 3 females from the vial with no locality and date given were labeled juveniles. The same explanation probably applies for the single specimen included in the type material of *T. sjoestedti* (12 males, 15 females, 1 juvenile). Both outer morphology and genitalia tell that these specimens are undoubtedly *C. togoensis*.

Cyclatemnus burgeoni (Beier 1932)

Material examined.—BELGIAN CONGO (DEMOCRATIC REPUBLIC OF CONGO): Kuri, terr. de Kabare, Bitale, 1600 m, 29 June 1951, N. Leleup leg. (RMCA, no. 110949–110950; Beier det.).

Cyclatemnus centralis Beier 1932

Material examined.—BELGIAN CONGO (DEMOCRATIC REPUBLIC OF CONGO):

Katanga, Terr. d'Alberville, mont. Kabobo, Ht. Kiymbi, 1700 m, September 1958, N. Leleup leg. (RMCA, no.112.741; Beier det.). RUANDA (RWANDA): 78 km W. of Astrida, 1957 (CAS; Beier det.).

Cyclatemnus dolosus Beier 1964

Material examined.—RHODESIA (ZIMBABWE): Northern Rhodesia, Abercorn, gallery forest, Riwer Mwengo, 8 miles N. of Abercorn, 1800 m, June 1960, N. Leleup leg. (RMCA, no.15.078; Beier [?] det.).

Cyclatemnus equestroides (Ellingsen 1906), NEW COMBINATION

Material examined.—EQUATORIAL GUINEA: Isl. Fernando Póo [Bioko], Punta Frailes, October 1901, L. Fea leg. (ZMUO, no. 217; syntype). PORTUGUESE GUINEA (GUINEA-BISSAU): Rio Cassine, February–April 1900, L. Fea leg. (ZMUO, no. 218; syntype).

Remarks.—Although these specimens are not labelled as type material, the collection details leave no doubt they form part of the type material used by Ellingsen (1906) in his description of the species. The remainder of the type material is deposited in the Museo Civico di Storia Naturale, Genova.

Beier (1932a, 1932b) placed this species in the genus *Tamenus*, but was clearly in doubt about this decision. After examining the specimens, it is quite clear that they do not belong in *Tamenus*. They lack a transverse groove on the carapace as Ellingsen (1906) himself pointed out, and the configuration of the trichobothria is different. On the other hand, these characters fit very well with those of *Cyclatemnus*. The difference between *C. equestroides* and the *Cyclatemnus* spp. investigated by me is that the palpal patella of *C. equestroides* is slightly broader seen in lateral view. The male genitalia are almost identical to those of *Cyclatemnus centralis*. Accordingly I transfer this species to the genus *Cyclatemnus*.

Cyclatemnus globosus Beier 1947

Material examined.—SOUTH AFRICA: E. Cape, Pirie Forest, March 1937, R.F. Lawrence leg. (NMP; Beier det.)

Cyclatemnus granulatus Beier 1932

Material examined.—IVORY COAST: Bingerville. 16 April 1962, J. Decelle leg. (RMCA, no. 121.999; Beier det.). CAMEROON: 10 mi. W. Bertona, 640 m, 5 October 1966, Ross & Lorentzen leg. (CAS; Beier det.).

Cyclatemnus minor Beier 1944

Material examined.—KENYA: Athi River, 1500 m, 19 October 1957, Ross & Leech leg. (CAS; Beier det.).

Cyclatemnus robustus Beier 1959

Material examined.—BELGIAN CONGO (DEMOCRATIC REPUBLIC OF CONGO): Tshibinda, February 1932 (RMCA, no. 54.233–54.234; Beier det.); Nioka, October 1953 (RMCA, no. 80.090; Beier det.). TANZANIA: TANGANYIKA?: 12.miles NE of Sumbawanga (RMCA, no. 116.008; Beier det.);

Micratemnus crassipes Mahnert 1983

Material examined.—KENYA: Nakuru, Lake Elmenteita, SS. pierres [under stones?], 1900 m, 7 November 1974, Mahnert & Perret leg. (MHNG; paratype).

Oratemnus loyolai Sivaraman 1980

Material examined.—INDIA: Tamil Nadu, Redhills, Madras, 6 August 1976 (MHNG; paratype); Tamil Nadu, Ganesaduram, N.of Coimbatore, 6 December 2000, K.R. Klausen & F. Klausen leg. (AUC; F. Klausen det.); Karnataka, Mysore, park by Ghandi Square, 29 November 2000, K.R. Klausen & F. Klausen leg. (AUC; F. Klausen det.). SRI LANKA: Peradeniya, Kandy District, Botanical Garden, 20 February 2000, D. Huber leg. (AUC; F. Klausen det.).

Oratemnus navigator (With 1906)

Material examined.—INDONESIA: Java, Batavia, March 1889, L. Loria leg. (ZMUO, no. 377; Ellingsen [?] det.); Bali, Brama Kutri, Singapadu, 12 March 1999, K.R. Klausen & F. Klausen leg. (AUC; F. Klausen det.); Between Papuan and Bantran, 10 March 1999, K.R. Klausen & F. Klausen leg. (AUC; F. Klausen det.). MALAYSIA: East Coast, 17 km N of Kuantan, 31 March 2002, F. Klausen leg. (AUC; F. Klausen det.).

As *Oratemnus brevidigitatus*: SEYCHELLES: Praslin, Cote d'Or, 30 July 1982, C.I. Voucher leg. (MHNG; Mahnert det.).

As *Oratemnus philippinensis*: PHILIP-

PINES: Luzon isl., Kiangan/Ifugao, 1982, Margraf leg. (SMNS, no. 1543; Schawaller det.).

As *Oratemnus saigonensis*: THAILAND: Doi Sutep, E slope, 260 m, 15 July 1962, E. S. Ross & D.Q. Cavagnaro leg. (CAS; Beier det.).

Remarks.—The material from the Zoological Museum in Oslo and the material collected by me on Bali and in Malaysia has been compared with the description given by With (1906) of *Oratemnus navigator* and the holotype from Zoological Museum in Copenhagen. There is no doubt that they are identical. Moreover, when Schawaller (1994) synonymized *O. saigonensis* with *O. semidivisus*, he suggested that *O. navigator* belongs to the same species together with *O. proximus*, *O. loyolai* and *O. yodai*. *Oratemnus loyolai* is definitely not conspecific with the others, judging from its very different and characteristic genitalia. However, the male genitalia of the others investigated by me are identical. Since the investigated specimens listed above of *O. brevidigitatus*, *O. philippinensis* and *O. saigoneneis* (= *O. semidivisus*) have been identified by very able specialists, there is a possible synonymy, perhaps together with *O. proximus* and *O. yodai*.

Oratemnus punctatus (L. Koch 1885)

Material examined.—AUSTRALIA: Queensland, 55 km N. of Goomeri, 23 January 1982, M. Baehr leg. (SMNS, no.898; Harvey det.).

Paratemnoides ellingseni (Beier 1932)

Material examined.—MOZAMBIQUE: Chitengo, Gorongoza Game Reserve, September 1957, R.F. Lawrence leg. (NMP, no. 5155; Beier det.). MADAGASCAR: Morondava, Betela Mission Station, 20 February 1998, Klausen leg. (AUC; Klausen det.). SOUTH AFRICA: Zululand, 1938 (NHMW; Beier det.); KZN, Gollel, August 1938, R.F. Lawrence leg. (NMP, no. 630; Beier det.); Lovedale, on trees (TMP, no. 4899; Judson det.). UGANDA: Apac District, Aboke, near St Marys College, 16 May 2002, Klausen leg. (AUC; Klausen det.); Kampala, Golf Course, 18 May 2002, Klausen leg. (AUC; Klausen det.).

As *Paratemnus pallidus* (in part): BELGIAN CONGO (DEMOCRATIC REPUBLIC OF CONGO): Garamba, 1951 (NHMW; Beier [?] det.).

As *Paratemnus braunsi*: ETHIOPIA: Bahar Dar, 12 October 1968, K.W. and H. Harde leg. (SMNS, no. 202; Beier and Mahnert det.).

Remarks.—The identification as *P. braunsi* raises the question of a possible synonymy. The species was placed in *Catatemnus* by Beier (1932a), obviously due to what he interpreted as a transverse furrow on the carapace. However, when Tullgren (1907) described the species based on one female, he explicitly wrote that "Querfurchen fehlen vollständig, nur auf der Mitte da, wo die zweite Furche sein sollte, bemerkt man einen kleinen Eindruck." In a paper by Weygoldt (1970), some of the material used and identified by Beier is referred to as *Paratemnus braunsi*, which suggests that Beier was aware of a misplacement in *Catatemnus*. So indicates this identification by Beier and Mahnert. The specimen investigated by me is decidedly a *P. ellingseni*, but since I have not investigated the type of *C. braunsi* deposited in the Natural History Museum in Hamburg, I leave it as a misidentification for the moment.

Paratemnoides insubidus (Tullgren 1907)

Material examined.—NAMIBIA: Kobos, 40 miles S of Rehoboth, 19 July 1937 (TMP, no. 7894; Beier det.).

Paratemnoides nidificator (Balzan 1888)

Chelifer nidificator Balzan, 1888a: no pagination, figs.

Chelifer (*Atemnus*) *nidificator minor* Balzan, 1892: 510–511, fig. 1. NEW SYNONYMY.

Material examined.—As *Paratemnus minor*: BRAZIL: Manaôs, 27 August 1973, R. Schuster leg. (MHNG, no. BR-331; Mahnert det.).

As *Paratemnoides nidificator*: BRAZIL: Mato Grosso State, Nova Mutum, Fazenda Buriti, 12 June 2003, H.F. Mendes leg. (AUC; Klausen det.); Sao Paulo, Riberto Preto, 4 June 2003, H.F. Mendes leg. (AUC; Klausen det.). COSTA RICA: near Ajugas, 5 December 1996, Klausen leg. (AUC; Klausen det.); Manuel Antonio, 8 December 1996, Klausen leg. (AUC; Klausen det.); Golfito, 9 December 1996, Klausen leg. (AUC; Klausen det.).

Remarks.—Balzan (1892) described *P. minor* as a variety of *P. nidificator*. He stated that *P. minor* is insignificantly smaller than *P.*

nidificator, but the palps and the chelal hand do not differ. Contrary to this he gave the body length of *P. minor* to be 4 mm (Balzan 1892) and that of *P. nidificator* to be 3 mm (Balzan 1890). With (1908) in his description of *P. nidificator* obviously considered *P. minor* as a variety of the former. Beier (1932a, 1932b) eventually raised *P. minor* to species level, stating that the two are very similar, although *P. minor* is smaller. The dimensions given of the palps and the fourth pair of legs are slightly smaller for *P. minor*, the ratio between lengths and widths are very close to *P. nidificator*.

I have examined 55 specimens, comprising five specimens of *Paratemnoides minor* from Manaôs, Brazil as given above, two specimens as *Chelifer nidificator* from Haiti (Tullgren det.), 16 from Sao Paulo, Brazil, 16 from Mato Grosso, Fazenda Buriti, Brazil and 16 specimens from the three localities in Costa Rica as given above. Admittedly, the specimens of *P. minor* and those from Costa Rica are slightly smaller compared to the average measures of those from the other localities identified as *P. nidificator*. However, the populations of *P. nidificator* from Mato Grosso and Sao Paulo both have specimens as small as those of *P. minor*. In other words the specimens of *P. minor* are within the range of *P. nidificator*. Moreover, when comparing the ratios between the lengths and widths of the individual segments of the pedipalps and the fourth legs, they are almost identical, no matter if they are taken from *P. minor* or *P. nidificator*. The outer morphological characters are identical, so are the genital characters of the males investigated. Thus there is no diagnostic character which separates them as two species. Accordingly I consider *P. minor* as a junior synonym of *P. nidificator*.

Paratemnoides pallidus (Balzan 1892)

Chelifer (*Atemnus*) *pallidus* Balzan, 1892: 511–512, figs. 2, 2a.

Chelifer (*Atemnus*) *guineensis* Ellingsen, 1906: 246. Synonymized by Harvey (1991).

Paratemnus congicus Beier, 1932b: 566–567, fig. 7. Synonymized by Beier (1972).

Paratemnus ceylonicus Beier, 1932b: 569, fig. 8. NEW SYNONYMY.

Material examined.—As *P. ceylonicus*: S-CEYLON (SRI LANKA): Habaraduwa, 20 January–4 February 1983, T. Osten leg. (SMNS, no. 1542; Schawaller det.).

As *P. congicus*: BELGIAN CONGO (DEMOCRATIC REPUBLIC OF CONGO): Brazzaville, 11 January 1964, Balogh & Zicsi leg. (MHNG, no. 653; Mahnert det.).

As *P. guineensis*: BELGIAN CONGO (DEMOCRATIC REPUBLIC OF CONGO): Brazzaville, 27 December 1963, Balogh & Zicsi leg. (MHNG, no. 589; Mahnert det.).

As *P. pallidus*: BELGIAN CONGO (DEMOCRATIC REPUBLIC OF CONGO): Garamba, 1951, (NHMW; Beier det.). UGANDA: Kampala, Golf Course, 18 May 2002, Klausen leg. (AUC; Klausen det.). SRI LANKA: Peradeniya, Botanical Gardens, Kandy District, 20 February 2000, D. Huber leg. (AUC; Klausen det.). MALAYSIA: Kuala Lumpur, 3 April 2002, Klausen (AUC; Klausen det.).

Remarks.—The descriptions given by Beier (1932a, 1932b) for *P. pallidus* and *P. ceylonicus* indicate that the main distinction is based on differences in the dimensions and proportions of the appendages. I have compared *P. ceylonicus* (13 specimens) from Sri Lanka and Malaysia with *P. congicus* and *P. guineensis* (2 specimens) from Belgian Congo and *P. pallidus* (8 specimens) from Uganda. I can find no significant differences in the pedipalps and the 4th legs of the two groups, either in dimensions or in proportions. Moreover, in his key to the genus *Paratemnus*, Beier (1932a, 1932b) used the length of the palpal finger compared to the width of the chela as a diagnostic character to separate *P. ceylonicus* (and *P. congicus*) from *P. pallidus*. In my material all the specimens have the fixed finger longer than the width of the palpal chela. In a later publication Beier (1972) synonymized *P. congicus* with *P. pallidus* which suggests that he no longer considered this to be a discriminating character. Based on my measurements and the fact that the male genitalia are identical, I consider *P. ceylonicus* to be a synonym of *P. pallidus*.

Paratemnoides salomonis (Beier 1935)

Material examined.—SOLOMON ISLANDS: Guadalcanal, 9 May 1965 (NHMW; Beier[?] det.). PAPUA NEW GUINEA: New Britain, Volo volo, 6 July 1995, K.R. Klausen & F. Klausen leg. (AUC; F. Klausen det.); Wevak, by Windjammer Hotel, 9 July 1995, K.R.

Klausen & F. Klausen leg. (AUC; F. Klausen det.).

Stenatemnus fuchsi (Tullgren 1907)

Material examined.—INDONESIA: Nias Island, Eastcoast, Lawalo, phoretic on Passalidae, 23 September 1979, D. Erber leg. (SMNS, no. 296; Schawaller det.); Sumatra [probably: Si-Rambé, 1891–94, E. Modigliani leg.] (ZMUO, no.538; Ellingsen det.).

Tamenus femoratus Beier 1932

Material examined.—IVORY COAST: Divo, 16 August 1963, J. Decelle leg. (RMCA, no. 83.161.132; Heurtault det.).

Titanatemnus gigas Beier 1932

Material examined.—CAMEROON: Bosum, scrub, 20 May 1914, Tessmann leg. (ZMB, no. 31190; paratype)

Titanatemnus natalensis Beier 1932

Material examined.—SOUTH AFRICA: Durban, March 1916, C. Akerman leg. (NMP, no. 5106; Beier det.).

As *Chelifer* (= *Titanatemnus*) *equester*: Natal, Durban, C.N. Barker leg. (ZMUO, no.553; Ellingsen det.).

Remarks.—The main difference between *T. natalensis* and *T. equester* is the size, with the latter being the larger of the two. Because size is not the best of criteria for separating species, an investigation of the genitalia of *T. equester* might give a clue to their relationship.

Titanatemnus palmquisti (Tullgren 1907)

Material examined.—Kenya: Meru, 25 April 1957 (NHMW; Leleup det.). NYASSA (MALAWI?): 1899, Fülleborn leg. (ZMUO, no. 306; identified by Ellingsen det.).

Titanatemnus sjoestedti (Tullgren 1901)

Material examined.—As *Chelifer sjoestedti*: CAMEROON: Itoki, February 1891, Y. Sjöstedt leg. (NRMS: syntype). FRENCH CONGO (CONGO): N'kogo, December 1902, L. Fea leg. (ZMUO, no. 211; Ellingsen det.).

Titanatemnus tessmanni Beier 1932

Material examined.—As *Chelifer sjoestedti*: PORTUGUESE GUINEA (GUINEA-BISSAU): Rio Cassine, January–April 1900, L. Fea leg. (ZMUO, no. 210; Ellingsen det.).

Titanatemnus thomeensis (Ellingsen 1906)

Material examined.—SAO THOMÉ: Agua Izé, 400–700 m, December 1900, L. Fea leg. (ZMUO, no.219; syntype).

The genital organs were dissected with honed steel needles under a stereomicroscope. Following 24 hours soaking in a solution of 2% pepsin in water acidified with HCl at room temperature, the organs were washed and placed in successive alcohol baths ending with a mixture of 96% alcohol and Euparal essence. I prefer this method to soaking in potassium hydroxide because it is probably more gentle to the delicate chitinized parts. The specimens were finally mounted on slides in Euparal.

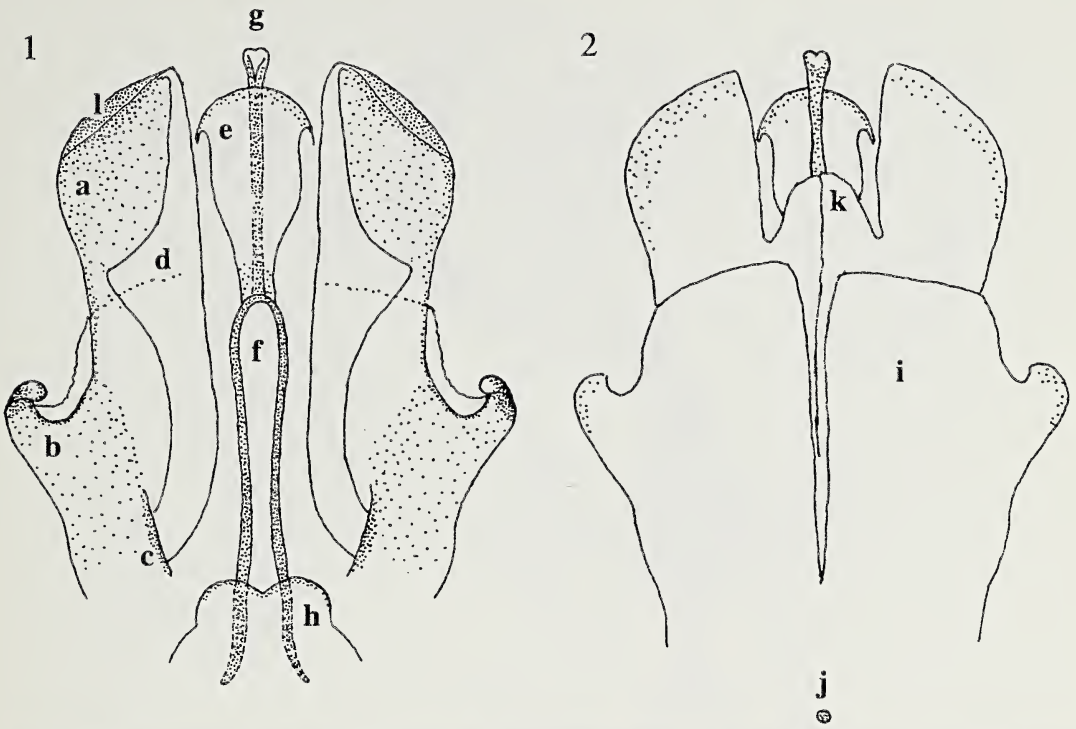
Specimens were examined and photographed under a stereomicroscope using darkfield/lightfield equipment. Drawings were made using a compound microscope with a drawing tube.

Dissection of the genital organs from the body was necessary because their orientation *in situ* makes it almost impossible to obtain a correct interpretation. Moreover, the translucent parts are particularly difficult to see in this position. All genital organs have accordingly been examined after dissection. They were orientated on the slide in a position with the lateral apodemes and lateral rods lying uppermost, horizontal to the light axis of the microscope.

DESCRIPTION OF THE GENITALIA

The description concentrates on the chitinized parts of the genitalia, i.e. the different diverticula of the genital atrium and their associated apodemes, as well as the ejaculatory canal and its atrium. Legg (1974) has given a generalized description of the genital organs of male pseudoscorpions. I have followed his terminology when possible.

The genital organ as a whole can be directed more or less anteriorly from the genital opening in some species and posteriorly in others. It is therefore confusing to use the terms dorsal and ventral side when referring to the different parts of the organ. To avoid confusion I use the term "anterior side" as the side of the organ which is connected to the anterior part of the genital aperture and "posterior side" for the side connected to posterior part of it (Figs. 3 & 4).



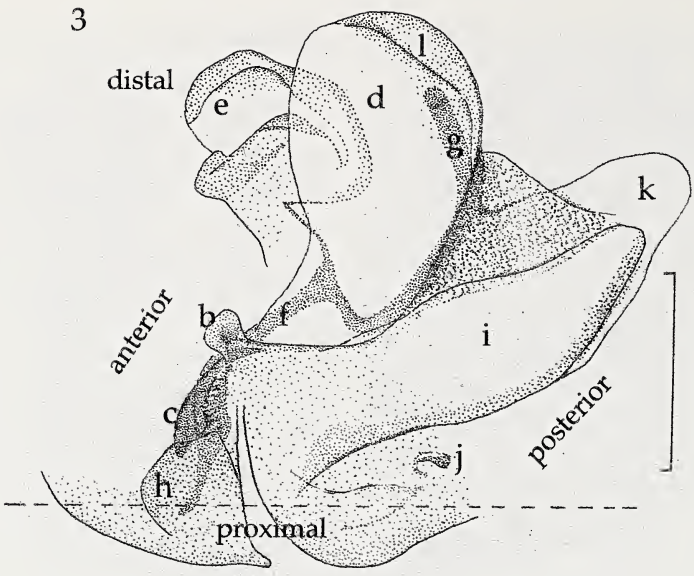
Figures 1–2.—Generalized view of atemnid male genitalia. Anterior side: a. lateral apodeme; b. hooked branch; c. sclerotized bar; d. longitudinal fold of medial diverticulum; e. ejaculatory canal atrium; f. lateral rods; g. dorsal apodeme; h. ventral diverticulum; l. lateral lip of lateral apodeme. Posterior side: i. dorsal diverticulum; j. apophysis of posterior dorsal gland; k. extension of medial diverticula.

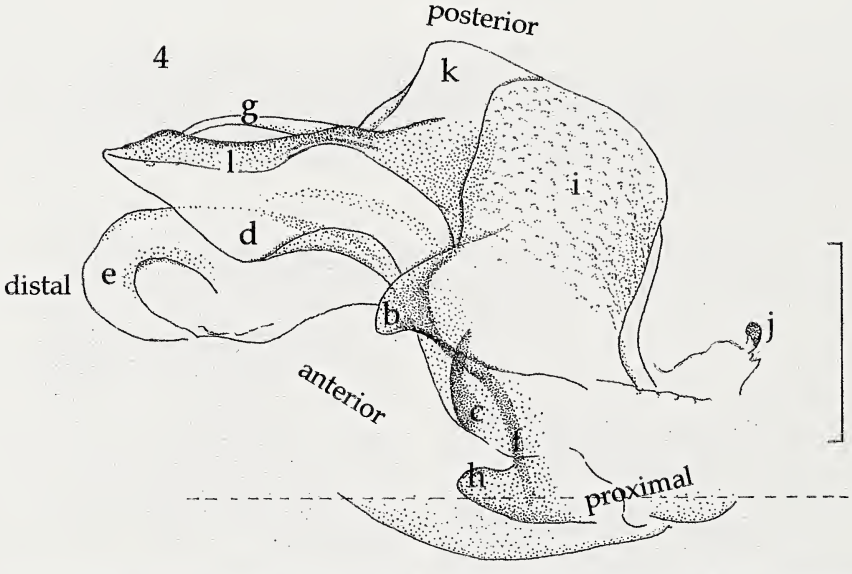
Moreover, I use the term "proximal" for the parts lying near the genital aperture and the term "distal" for parts near the seminal vesicles (Figs. 3 & 4). However, when the words are part of established terms, like in "dorsal diverticulum" or "dorsal apodeme", I have kept them to make my descriptions compatible with that of Legg (1974).

The size of the genital organ is correlated with the size of the species: the larger species like *Titanatemnus* (Figs. 11–14) have the most prominent organs with distinctly colored apodemes; in the smaller species of *Paratemnoides* (Figs. 18–20), *Brazilatemnus* and *Stenatemnus* (Figs. 6 & 10) the organ is small, transparent and almost colorless. The specimen of *Anatemnus javanus* (Fig. 24) studied is completely colorless, but this is probably due to conservational conditions.

The most conspicuous parts on the anterior side of the organ are the lateral apodemes and the lateral rods, connected to the dorsal apodeme and the ejaculatory canal atrium (Fig.1). The posterior side is dominated by the prominent and translucent bilobed *dorsal and medial diverticula* lying side by side along the sagittal plane (Fig. 2).

Dorsal diverticula (Figs. 2, 3 & 4: i).—On the posterior side of the genital organ the proximal part of the dorsal diverticula is connected to the atrium of the posterior dorsal gland with its support and rugose entrance area. The posterior dorsal gland is attached to this area which has a small, knob-shaped apophysis (Figs. 2, 3 & 4: j). Distally the dorsal diverticula are confined by a transverse fold overlying the medial diverticula and running between the hooked branches of the two lateral apodemes (Figs. 1, 3 & 4: b). On the lateral side of the dorsal diverticula the surface is very rugose. It is made up of a dense layer of more or less conical tubercles, each with a minute hole in the utmost tip. They obviously are the seat of glands, like the entrance area of the posterior dorsal gland. In most species the dorsal diverticula are almost fused in the sagittal plane on the posterior side. The dorsal diverticula are extended lat-



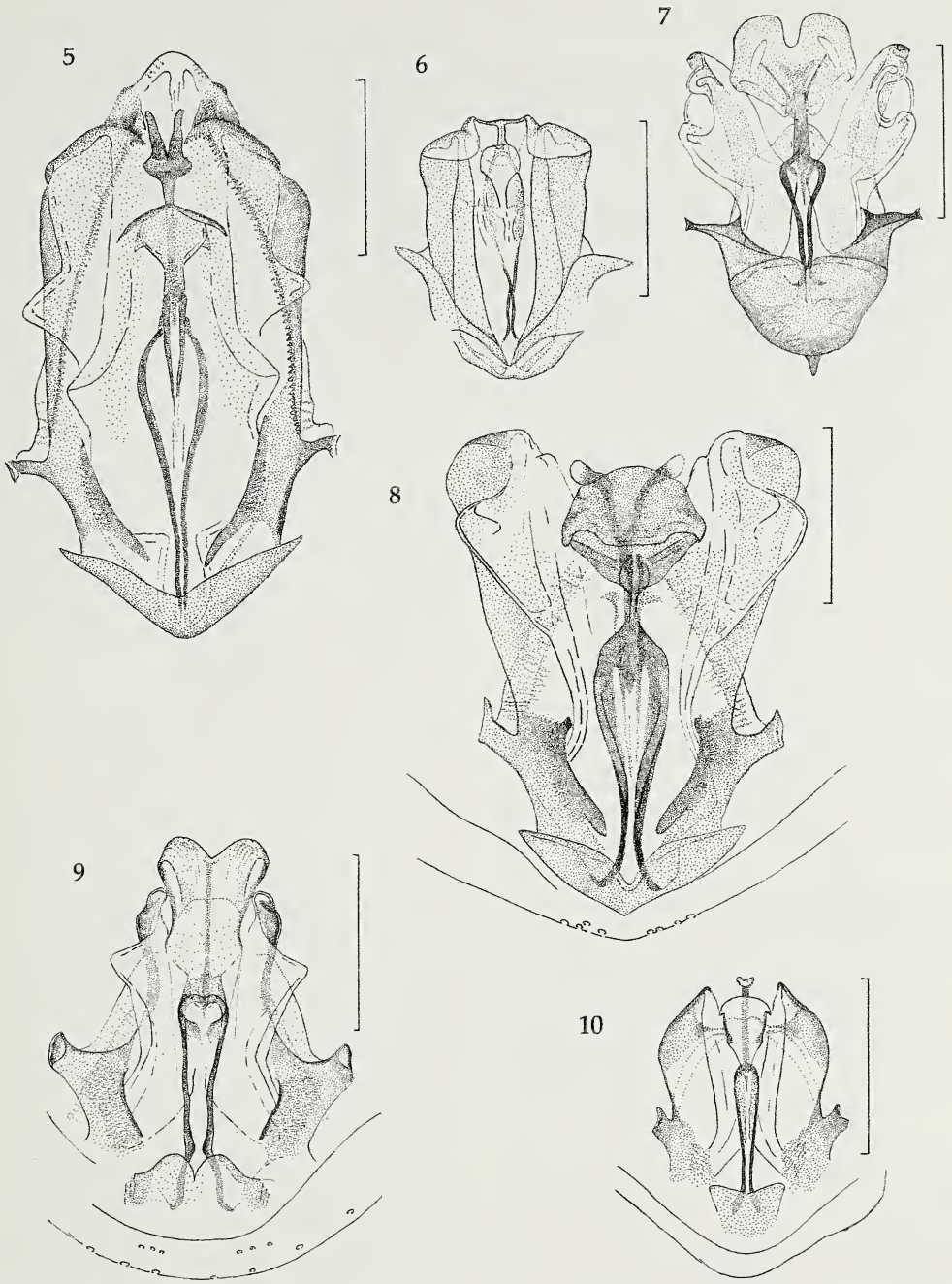


Figures 3–4.—Male genitalia, left lateral view: 3. *Diplotemnus insolitus*; 4. *Paratemnoides ellingseni*. Scale lines = 0.2 mm; abbreviations as in Figs. 1–2.

erally and enfold the proximal part of the medial diverticula on the anterior side. Here the dorsal diverticula are dominated by the lateral apodemes with their hooked branches.

Medial diverticula (Figs. 1, 2, 3 & 4: d, k).—Distally the medial diverticula extend beyond the dorsal diverticula to the level of the ejaculatory canal atrium. Here they are mostly made up of the lateral apodemes.

In many species the two medial diverticula have a prominent *extension* along the sagittal plane on the posterior side of the genital organ (Figs. 2 & 3: k). Both of these extend to the level of the ejaculatory canal atrium and are fused along the midline, forming a finger-like bulge. This is easily seen from the anterior side for instance in *Titanatemnus gigas*, *T. tessmanni*, *Cyclatemnus centralis* and *Cata-*



Figures 5–10.—Male genitalia, anterior side: 5. *Miratemnus hirsutus*; 6. *Brazilatemnus browni*; 7. *Tullgrenius indicus*; 8. *Diplotemnus insolitus*; 9. *Atemnus politus*; 10. *Stenatemnus fuchsi*. Scale lines = 0.2 mm.

temnus togoensis (Figs. 11, 14, 21, 28). In *Diplotemnus insolitus* it is pointed posteriorly and can best be seen from the lateral side (Fig. 3: k). In *Oratemnus loyolai* it is very conspicuous and protrudes beyond the lateral apodemes (Fig. 15). In others like *Paratemnoides* and *Tullgrenius indicus* this extension is reduced or almost lacking (Figs. 4k, 7, 18–20, 22). Proximally, the medial diverticula are covered by the dorsals and their associated lat-

eral apodemes on the anterior side of the genital organ.

On the anteromedial side the membranous wall of both the medial diverticula is folded-over, forming a longitudinal fold running from the distal end of the lateral apodeme right up to the proximal part of the same (Fig. 1d). Here the fold is covered by the lateral apodeme (Fig. 1c). In most genera the fold has a projection midway along its length. This can be distinctly pointed, as for instance in *Miratemnus hirsutus*, *Atemnus politus*, *Titanatemnus palmquisti* and *Cyclatemnus centralis* (Figs. 5, 9, 12, 21). In *Oratemnus navigator* the pointed projection typically has a small indentation (Fig. 16). *Catatemnus birmanicus* and *C. granulatus* have the projection of the longitudinal fold more gently rounded, and in the latter species it has a distinct notch (Figs. 26, 27). In others, like *T. gigas*, *T. sjoestedti*, *T. tessmanni* and *Anatemnus voeltzkowi* the projection is more like a lobe (Figs. 11, 13, 14, 25). *Tullgrenius indicus* is aberrant in having two lobes (Fig. 7) as is *Anatemnus novaguineensis* in having three overlapping lobes (Fig. 23). In *Brazilatemnus browni*, *Stenatemnus fuchsi*, *Paratemnoides pallidus*, *P. nidificator* and *P. salomonis* (Figs. 6, 10, 18–20) the projection of the longitudinal fold is lacking.

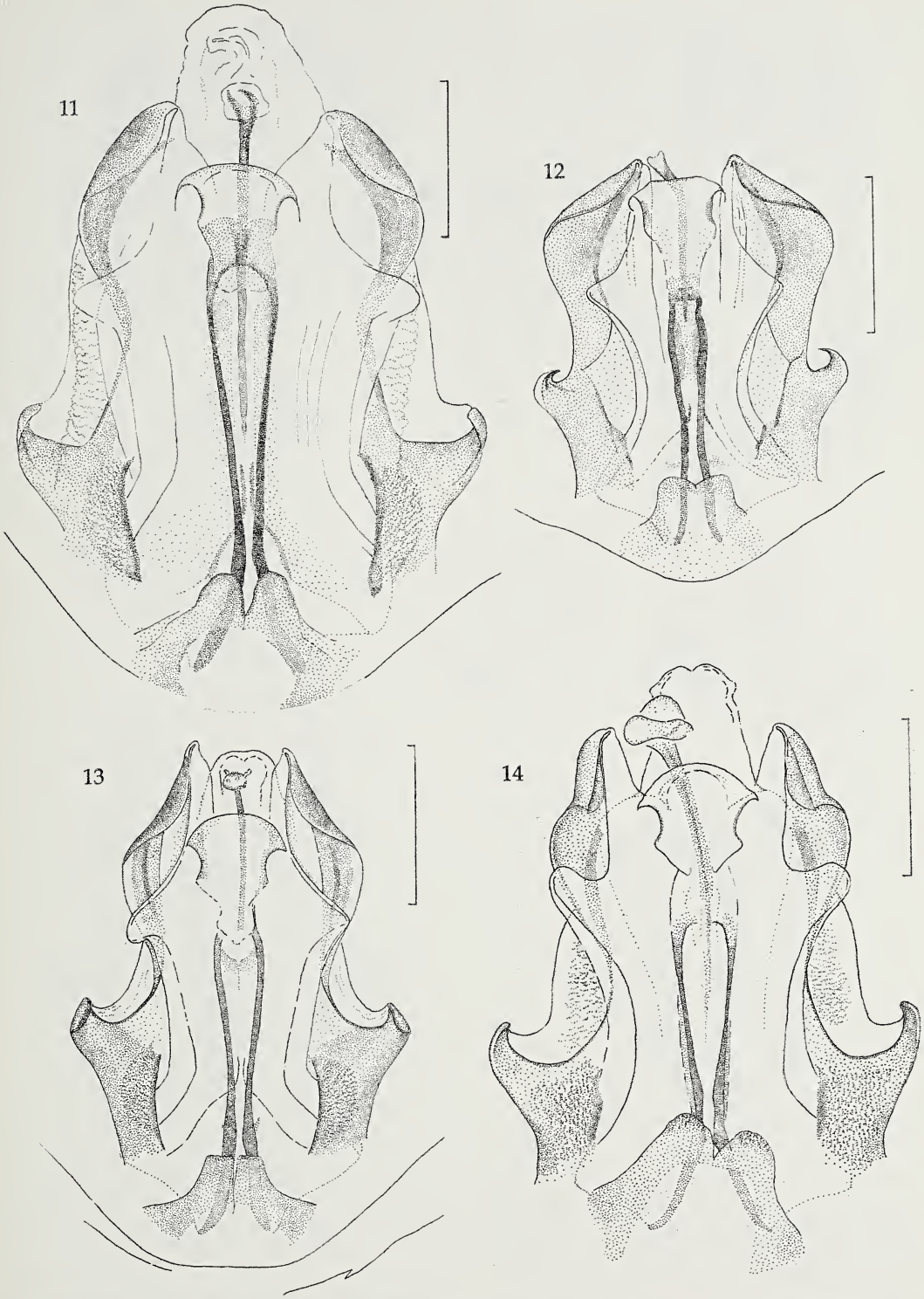
Ventral diverticulum (Fig. 1: h).—The anterior wall is mostly sclerotized, but can be colorless and almost transparent in some of the smaller species. Typically it is bilobed, most pronouncedly so in the *Titanatemnus* species (Figs. 11, 13, 14). In the four miratemnine genera this diverticulum is very wide and has a somewhat hood-like appearance (Figs. 5–8)

Lateral apodemes (Fig. 1: a).—The lateral apodemes are sclerotized regions formed by the anterolateral side of the two dorsal and medial diverticula. The apodemes run along either side of the lateral rods. The apodemes are oriented parallel to the rods but can be differently shaped in the different species. This is most marked at the distal end. Generally they are distinctly colored and sclerotized in the larger species, whereas in the smaller species they are delicate and almost colorless.

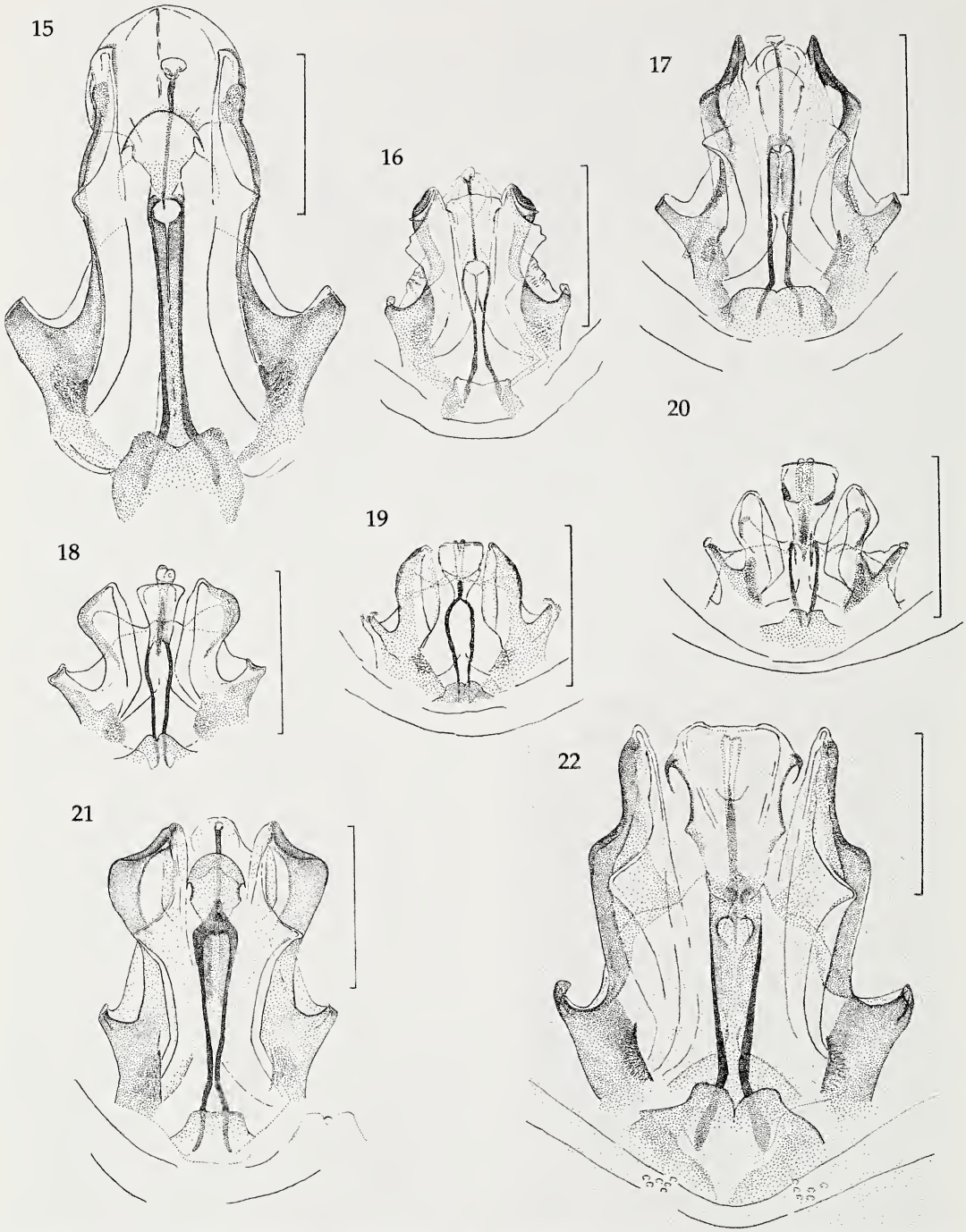
The lateral apodemes can be divided in 2 principal parts: A proximal part situated on the dorsal diverticula characterized by a *hooked branch* situated on the lateral side. In the miratemnines *Miratemnus hirsutus*, *Brazilatemnus browni* and *Tullgrenius indicus* (Figs. 5–7), the hooked branch forms an almost straight stub perpendiculary to the axis of the whole organ, less so in *Diplotemnus solitus* (Fig. 8). In the atemnines this branch is bowed distally. In both Miratemninae and Atemninae it always terminates in a plate-like tip, perhaps with the exception of *B. browni*. This can be very pronounced as in *Atemnus politus*, *Titanatemnus gigas*, *Paratemnoides ellingseni* and *Anatemnus voeltzkowi* (Figs. 9, 11, 22, 25). This tip is the only part of the lateral apodemes which has muscles attached to it. The proximal part always has a sclerotized rugose area on either side of the sagittal line (Fig.1c). It is often delimited on the medial side by a darker bar. The function of this might be to reinforce the lateral apodeme when subjected to muscular contractions. In species with smaller genitalia this bar is colorless and probably reduced.

A distal part situated on the medial diverticula and more or less expanded laterally. This part of the lateral apodemes takes a wide range of different forms, being the most variable from one species to another. Though this part can be very variable it always has a *lateral lip* which is either bowed, rolled or wrapped up (Fig. 1l). In *Titanatemnus gigas* it is almost like a spoon; in *Oratemnus punctatus* and *Cyclatemnus centralis* it has the same shape but is bowed concavely (Figs. 11, 17 and 21). *Catatemnus birmanicus*, *Anatemnus voeltzkowi*, *A. angustus* and *A. orites* have a distinct inner ridge bowed into a semicircle, which make them stand apart from the others (Figs. 25, 26). In *P. ellingseni* the lateral lip is rolled into a tube (Figs. 4a, 22). In the other *Paratemnoides* and in *Stenatemnus fuchsi* the lateral lip is diminutive, almost lacking (Figs. 10, 18–20). In *Atemnus politus* the distal part is proportionally smaller, as is the case for *Catatemnus togoensis* (Figs. 9, 28) and *Micratemnus crassipes*. In the miratemnines the lateral lip is transversely directed. The same is true of *Anatemnus novaguineensis* and *A. javanus*, but here as if the whole genital organ has been compressed in a longitudinal direction (Fig. 23, 24).

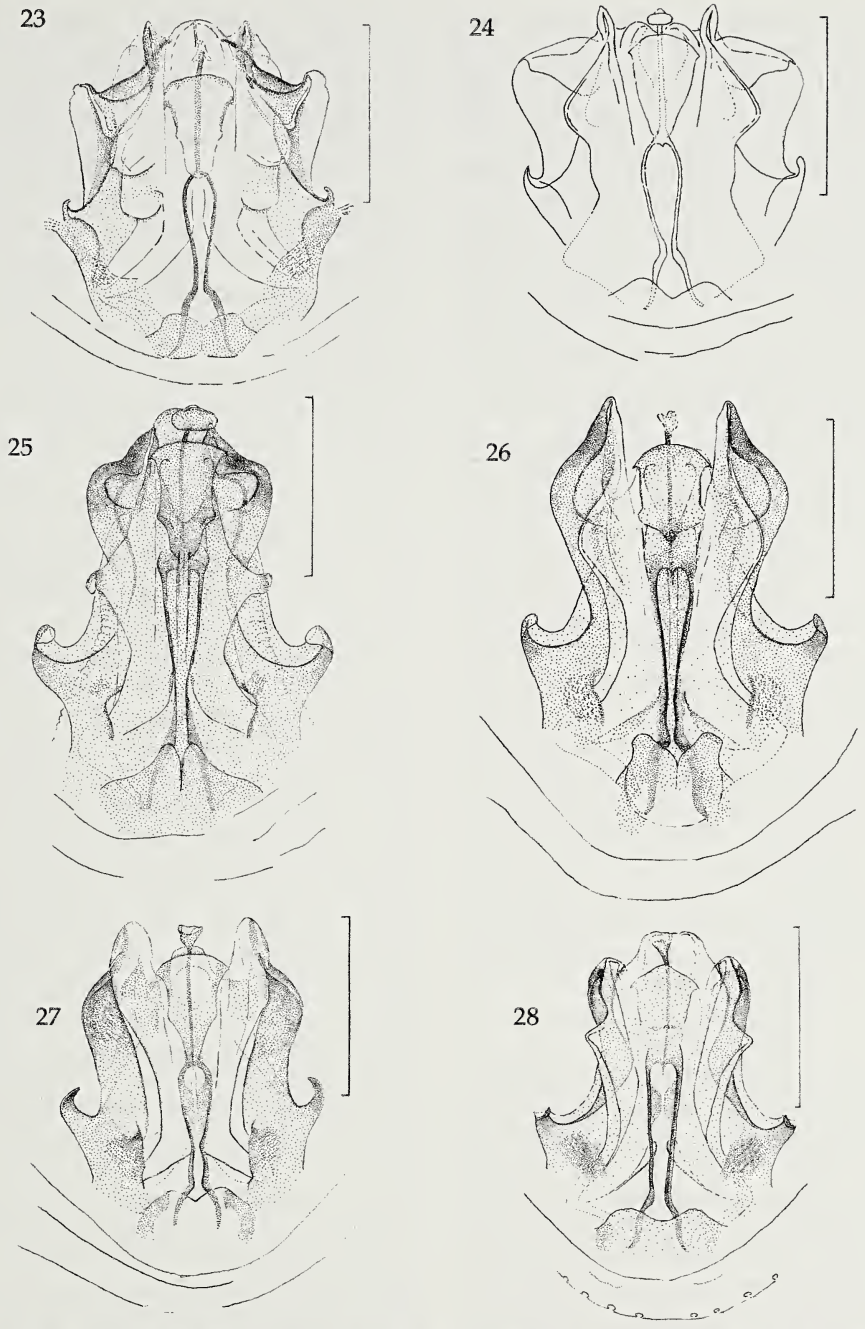
Lateral rods (Fig. 1: f).—Lateral rods, which flank the ejaculatory canal, are present in all species examined. The tips of their ends



Figures 11–14.—Male genitalia, anterior side: 11. *Titanatemnus gigas*; 12. *T. palmquisti*; 13. *T. sjoestedti*; 14. *T. tessmanni*. Scale lines 0.2 mm.



Figures 15–22.—Male genitalia, anterior side: 15. *Oratemnus loyolai*; 16. *O. navigator*; 17. *O. punctatus*; 18. *Paratemnoides pallidus*; 19. *P. nidificator*; 20. *P. salomonis*; 21. *Cyclatemnus centralis*; 22. *P. ellingseni*. Scale lines = 0.2 mm.



Figures 23–28.—Male genitalia, anterior side: 23. *Anatemnus novaguineensis*; 24. *A. javanus*; 25. *A. voeltzkowi*; 26. *Catatemnus birmanicus*; 27. *C. granulatus*; 28. *C. togoensis*. Scale lines = 0.2 mm.

are always placed inside the ventral diverticulum. Here the tips diverge, except in *Miratemnus hirsutus* and *Paratemnoides pallidus*, *P. nidificator* and *P. salomonis* (Figs. 5, 18–20). In most cases the lateral rods are bowed when seen from the anterior side, forming a lyre-like structure before they fuse with the dorsal apodeme. Seen from the lateral side, they are mostly recurved as in *P. ellingseni* (Fig. 4f) or may be bent in a procurved angle as in *D. insolitus* (Fig. 3f).

Dorsal apodeme (Fig. 1: g).—The dorsal

apodeme is bowed in the sagittal plane, running from the lateral rods in a curve around the ejaculatory canal atrium (Figs. 3g, 4g). This structure seem to be made up of the fused elongation of the two lateral rods. In the miratemnines it is distinctly bifid at the distal end, very prominent in *Miratemnus hirsutus* and *Diplotemnus insolitus* in which the dorsal apodeme is shaped like a narrow rake with two prongs (Figs. 5, 8). In the atemnines the two distal tips are almost completely joined, but can always be identified as two minute spikes or knobs lying side by side, as for instance in *T. gigas* and *P. pallidus* (Figs. 11, 18). The apodeme is distinctly colored proximally, but more or less transparent at the distal end. Muscles are connected to the distal end.

Ejaculatory canal atrium (Fig. 1: e).—The atrium of the ejaculatory canal covers the prostatic reservoir. It is bowl or cup shaped when seen laterally, fairly simply constructed in the atemnines, but more elaborate in the miratemnines (Figs. 3e, 4e). When seen from the anterior side, the atrium of the atemnines is more or less crescent-shaped on either side, marking the openings for the incoming ducts of the seminal vesicles. The distal end of the atrium is typically either procurved or flattened in the atemnines. The atrium of *Atemnus politus* is aberrant in this respect (Fig. 9). In the miratemnines the configuration of the atrium seems to differ more between the genera than is the case in the atemnines.

DISCUSSION

Characters diagnostic of the family.—The male genitalia of the Atemnidae share common features which make them stand apart from other pseudoscorpion families. Compared to the other families of the Cheliferoidea, they clearly constitute a monophyletic group in this respect. The characters which unite them can be summed up in the following diagnostic description. The letters refer to those of Figs 1 and 2: (a) Distal part of lateral apodemes more or less sclerotized, especially the lateral border. The lateral border is always bowed,wrapped or rolled-up in a lateral lip, sometimes to the extent of giving the lateral apodeme a snout- or rod-like appearance; (b) Proximal part of each lateral apodeme with a hooked branch laterally. Typically these are sclerotized, but when reduced they are translucent and hard to see; (c) Proximal part of each lateral apodeme furnished with a rugose darker area and delimited by a bar medially, strengthening this area; (d) Medial diverticulae more or less wrapped up on the anterior side along the sagittal line and overlying the lateral apodemes, often with a pointed or rounded projection midway; (e) Atrium of the ejaculatory canal more or less bowl-shaped; (f) Lateral rods long and conspicuous, running parallell to the sagittal line. Usually diverging proximally; (g) A long dorsal apodeme is always present, made up of the fused elongation of the lateral rods. Bifurcate or bilobate distally; (h) Anterior wall of the ventral diverticulum bilobed or bipartite; (i) Distal part of the two dorsal diverticulae are folded transversally making up the border against the medial diverticulae on the posterior side; (j) A knob-shaped apophysis present, which may have an attachment function for the posterior dorsal gland.

Affinities to other families.—The Atemnidae including the Miratemninae are placed in the Cheliferoidea together with the Cheliferidae, Chernetidae and Withiidae. Harvey (1992) dealt with the affinites between these four families and placed the first three in a trichotomy because he could not find any apomorphies that might split this group in smaller entities. Proctor (1993) has pointed to the fact that the spermatophore stalk of the Cheliferidae and the Chernetidae possess a droplet that is absent in the Atemnidae and the Withiidae. This resolves the trichotomy and places the Cheliferidae and Chernetidae in a clade separated from the other two. Although this does not imply any closer connection between the atemnids and the withiids, it might be noted that the overall configuration of the male genitalia of atemnids seem to be closer to the withiids than to the other two families.

In Chernetidae the almost circular apodemes have the distal ends fused or united, this configuration seem to be very consistent and very different from that of the atemnids. The absence of lateral rods in the chernetids also make them stand apart from the atemnids.

When considering the Cheliferidae there are some similarities. They have the same long, parallel lateral rods as the Atemnidae but there is one significant difference, at least when compared to *Chelifer cancroides* and *Dactylochelifer latreillii* as pictured by Vachon (1938a) and Legg and Jones (1988). This is

that the proximal ends of the lateral rods are merged in the cheliferids, which is never the case in the atemnids investigated by me. Another very important difference between the two families is the presence of ram's horn organs in the cheliferids, which are absent in the atemnids.

This leaves us with the Withiidae, which has the long, parallel lateral rods not merged proximally, just as in the Atemnidae. Moreover, the lateral apodemes of the withiids have the same pronounced hooked branches as in the atemnids, as shown by Heurtault (1971) and Harvey (1988). Judged from these character states of the male genitalia, I consider the Withiidae as the sister group to the Atemnidae.

Differences between Atemninae and Miratemninae.—Despite the differences between the genera and between the species, the overall structures of the male genitalia and their orientation are remarkably uniform in atemnines and miratemnines. However, because the miratemnines have earlier been raised to family level partly because of certain characteristics of their male genitalia, it seems appropriate to discuss their affinities here.

When Vachon (1938a) compared the male genitalia of *Titanatemnus congicus*, *Atemnus politus* and *Catatemnus schlottkei* with those of *Miratemnus hispidus*, he concluded that the apodemes of the latter differed in being directed in the opposite direction to those of the former. He also concluded that in this respect *Miratemnus* came closer to *Withius* than to the other three. Dumitresco & Orghidan (1969, 1970) used this as an important argument in favor of raising the miratemnines to family level.

However Vachon's observations on atemnines and miratemnines are not based on fundamental differences in the structure of the genitalia or in the mutual arrangement of these structures, a fact that Vachon certainly must have been aware of. The differences simply depend on the orientation of the genitalia. When examined in situ, the genitalia of the atemnines *Titanatemnus* and *Atemnus* are bent anteriorly from the genital opening, whereas those of *Miratemnus* are bent posteriorly. In a ventral view, then, in the atemnines one actually observes the organ with the anterior side lying nearest to the sternites, while in the miratemnines *Miratemnus* and *Diplotemnus* one has the posterior side nearest to the sternites, as shown by the side view of *Paratemnoides ellingseni* and *Diplotemnus insolitus* (Figs. 3, 4).

Hence, the crucial point is whether this difference in bending is sufficient to justify a separation into two families. In fact, this difference is not absolute between the two groups. The miratemnine *Tullgrenius* has an organ in which the distal part is bent at a 45° angle anterior to the genital aperture and in the Asiatic and American atemnids of the genus *Paratemnoides* the whole organ is directed almost dorsoventrally. Harvey (1988) observed that the orientation of the lateral rod in *Paratemnoides assimilis* was more similar to Miratemninae than to the atemnines *Atemnus* and *Titanatemnus*. Obviously the angle of the genitalia varies in both atemnines and miratemnines and does not provide a useful diagnostic difference between the groups.

Even if there are no fundamental differences separating the miratemnines and atemnines, the morphology of the male genitalia of miratemnines shows characteristics which separate them from the atemnines. These might be used as diagnostic character states of the miratemnines. They can be summarized as follows: (a) The anterior wall of the ventral diverticulum is very wide, covering the most proximal part of the lateral apodemes and having a hood-like appearance.(b) The hooked branch of the lateral apodemes is straight when seen from the anterior side, mostly perpendicular to the longitudinal axis of the whole organ.(c) The distal end of the dorsal apodeme is distinctly bifurcated into two separate branches, which are not merged as in the atemnines.

Differences between genera.—The investigation of the genitalia of the different species reveals a very striking result. The variation between the different species within a genus is often greater than the variations between species from different genera. The obvious explanation must be that several of the genera are not monophyletic. The reason for this might be that the delimitation of the genera is based on external morphological characters which in some cases are difficult to observe and of dubious diagnostic value. This relates to both discrete and continuous characters. For instance, size is used by Beier (1932a, 1932b) as a diagnostic character to separate *Titana-*

temnus from *Cyclatemnus* and *Paratemnoides* and *Oratemnus* is separated from *Atemnus*, *Anatemnus* and *Micratemnus* by the slimmer stalk of the patella.

Another important diagnostic character is the presence or absence of a transverse groove or furrow on the carapace. This is used as a major distinguishing feature to separate several genera of Atemninae. According to Beier (1932a, 1932b) those atemnines with a groove are *Catatemnus*, *Metatemnus*, *Stenatemnus* and *Tamenus*. This follows the original description by Thorell (1889) of *Chelifer birmanicus* (the type species of *Catatemnus*) where he states that the carapace has a "sulco transverso singulo", i.e. a single transverse groove or furrow. This groove can be very difficult to define, and any slight depression on the carapace might have been interpreted as a groove. This problem is discussed by With (1906) who makes a distinction between groove, stripe and line; in *C. birmanicus* he described this character as a transverse stripe and in *C. concavus* and *C. monitor* as a transverse line, all three later included in the genus *Catatemnus* by Beier (1932a, 1932b). In fact, when scrutinized, the transverse stripe of *C. birmanicus* actually is the borderline between the dark colored frontal part and the pale posterior part of the carapace, at least in those syntypes which have been available to me deposited in Naturhistoriska Riksmuséet in Stockholm and in Zoological Museum in Copenhagen. The absence of a furrow or groove is particularly obvious when the specimens are looked at from the lateral side, seeing the outline of the carapace.

However, in several other species where the specimens are prepared, a sort of transverse fold can be observed in the same area, as if a narrow part of the anterior of the carapace is wrapped over the posterior. Specimens of *Catatemnus togoensis*, *C. granulatus*, *Tamenus femoratus* and *Stenatemnus fuchsi* show this fold. Another species, *Micratemnus crassipes*, does have a transversal fold, although the genus was originally described as being without a groove on the carapace. The same fold is pronounced in *Miratemnus* and *Diplotemnus* but very weak or absent in *Tullgrenius*, although the groove as such is evident in all Miratemninae. On the other hand, the syntype of *Catatemnus birmanicus*, the type species of that genus, definitely does not have a fold. To sum up, this character is obviously not a discrete one, but varies through different phases from a very distinct groove accompanied with a fold, to a groove or slight depression with no fold or to a fold with no groove; or just a difference in color and sclerotisation between the anterior and posterior part. This diversity might be looked at as the different expressions of the vestigial border between the head and the first segment of the carapace.

Variation within genera.—*Anatemnus species (Figs. 23–25):* Of the three species figured here, *A. javanus* (the type species) and *A. novaguineensis* seem to constitute a group with synapomorphic character states. Their peculiar shape, as if the whole organ has been compressed in a longitudinal direction, distinguishes them from all other species compared here. This compression has placed the lateral lip in an almost transversal position, ending in a small projecting snout at the distalmost end. Another shared characteristic which makes them stand apart from other species is their comparatively small hooked branches. *Anatemnus subvermiformis* has the same transversally placed lateral lips but lacks the projecting snout and has the same small hooked branches. There can be no doubt that these three species are closely related. *Anatemnus elongatus* has the same transversally directed lateral lips and the same projecting snout at the distalmost end as in *A. javanus* and *A. novaguineensis*, but it has the hooked branches projecting wider to each side.

In contrast, *A. voeltzkowi* has the lateral apodemes quite differently shaped. The lateral lips of this species have a strongly curved medial border, shared with *Catatemnus birmanicus* and *A. angustus*. The shape of the ejaculatory canal atria is also very similar. Although the shape of the ventral diverticulum and the projection of the longitudinal folds are different and more reminiscent of those of *Titanatemnus*, the overall similarity indicates a closer connection between these two species than existing systematic positions implies.

Anatemnus angustus is identical to *C. birmanicus* in genital configuration as well as in external morphology, apart from carapace, as noted in the species list. The male genitalia of *A. orites* are very similar to *A. angustus*. The only difference is that the whole organ of *A. orites* is slightly slimmer across the lateral lips

of the lateral apodemes and their lateral incurvation are less pronounced than in *A. angustus*. Taking all this into account the genus *Anatemnus* seems to be polyphyletic. At least, based on the male genitalia, it can be roughly divided into two groups, one very close to *C. birmanicus* and another standing apart from all other species investigated.

Catatemnus species (Figs. 26–28): This is another genus in which there are few common features in the character states of the genitalia. The ventral diverticulum of *Catatemnus granulatus* and *C. togoensis* are similar but differ from the more deeply bilobed ventral diverticulum of *C. birmanicus* (the type species). The longitudinal folds of the medial diverticula are different in all three species, as are the lateral lips of the lateral apodemes and the ejaculatory canal atria do not have any striking resemblances. However, when external morphology is considered, both *C. granulatus* and *C. togoensis* have a transverse fold on the carapace, which is lacking in *C. birmanicus*. The trochanter of the pedipalps has a rounded dorsal bulge in the former two, whereas in *C. birmanicus* this bulge is pointed. Seen in lateral view, the patella is bulb- or vase-shaped in *C. birmanicus*, but in *C. granulatus* and *C. togoensis* it is more elongated and spindle shaped. On the other hand the presence of discal seta on the tergites of all three species might indicate relationship.

In this context it is worth noticing that *Tamenus femoratus* has the transverse fold on the carapace, present in *C. granulatus* and *C. togoensis* but lacking in *C. birmanicus*. The genitalia have the characteristic configuration of the lateral lip seen in *C. birmanicus* and *Anatemnus voeltzkowi*, even if the lateral border is almost straight rather than incurved, more like that in *A. orites*. The ventral diverticulum of *T. femoratus* is distinctly bilobed, much as in *A. voeltzkowi*, but the longitudinal fold is almost straight with a small fin-like projection midway, not gently curved as in *C. birmanicus* and *A. voeltskowi*. Another species worth mentioning in connection with *Catatemnus* is *Micratemnus crassipes*. This species have genitalia with a strong recemblance to *C. togoensis*, especially the distal part of the lateral apodeme, even if the whole organ is smaller and corresponding to the smaller size of the animal.

Cyclatemnus species (Fig. 21): The species *C. burgeoni*, *C. dolosus*, *C. globosus*, *C. granulatus* and *C. robustus* have genitalia almost identical to those of *Cyclatemnus centralis* (the type species), as does *C. minor* although these are smaller. The differences between them are confined to slight variations in the curvature of the lateral lips of the lateral apodeme. At least when considering the male genitalia, this genus seem to be very homogenous. However, *C. granulatus* is divergent in its external morphology. It has discal seta on tergites IV–X, as in *Catatemnus*, this is in accordance with the observation of Vachon (1952). The other species lack the discal seta on the tergites IV–VIII, which contradicts the observations of Mahnert (1983) on *Cyclatemnus centralis*.

Athleticatemnus pugil (the type and sole species) bears a strong likeness to *C. granulatus* in external morphology as noted earlier. The genitalia of *A. pugil* resemble those of *Cyclatemnus*, but the curvature of the distal part of the lateral apodeme is more straight angled, the lateral lip is slimmer and the most distal part of the lip is drawn up in a dorsoventral direction.

Oratemnus species (Figs. 15–17): It is hard to find any common denominators in the genitalia of the three species treated here that might be called apomorphic character states and thus make them stand apart from the others as a single entity. They all have a rather shallow bilobation of the ventral diverticulum but then so have several others, such as *Stenatemnus fuchsi*, *Catatemnus granulatus* and *C. togoensis*. The ejaculatory canal atrium of *O. loyolai* is reminiscent of that of *Cyclatemnus centralis*, whereas that of *O. punctatus* is more like the atrium of *Anatemnus javanus* or *Stenatemnus fuchsi*. The atrium of *O. navigator* is intermediate between that of *Anatemnus novaguineensis* and *Catatemnus togoensis*. The most divergent character among the three is the configuration of the lateral lips. *Oratemnus punctatus* has the lateral lip formed almost like those of *Cyclatemnus* or *Titanatemnus*, in fact, the organ as a whole might easily be that of a *Cyclatemnus* species. The lateral lips of *O. loyolai* do show some resemblance to those of *Paratemnoides ellingseni*, but *O. loyolai* differs clearly in the bulging shape of the medial diverticular extension. *Oratemnus navigator* stands apart from the other two in having a very small lateral lip

and by having an additional fin in front of the projection of the longitudinal fold. In its external morphology *O. navigator* differs mostly in having discal seta on the tergites, which are absent in the other two. Judged from the configuration of the male genitalia in the three species I have investigated, the genus *Oratemnus* seems to be polyphyletic.

Paratemnoides species (Figs. 4, 18–20, 22): In this genus the three species *P. nidificator*, *P. pallidus* (the type species) and *P. salomonis* are very much alike; they are only separated by minor differences in the proportions of the hooked branch and the distal part of the lateral apodeme. Although the differences are small they seem to be very constant in the specimens investigated by me, indicating that they are specific. The aberrant species is obviously *P. ellingseni*, which clearly stands apart from the others in the configuration of the genitalia. Except for the size alone, the shape of the lateral apodemes are totally different, the longitudinal fold has a pronounced projection, the lateral rods are diverging proximally inside the ventral diverticulum, and the ejaculatory canal atrium has crescent shaped openings on either side which are lacking in the other *Paratemnoides*. Considering these characters, it is hard to believe that *P. ellingseni* could be congeneric with the others. The external morphology is indeed very similar, which of course is the main reason that this species has been placed in *Paratemnoides*. However there are some differences: the trochanter of *P. ellingseni* has a pointed bulge dorsally, whereas in the others this bulge is less pronounced and rounded; the shape of the patella in lateral view is almost flattened in *P. ellingseni*, like a short sausage, whereas in the others it is bean-shaped. The last species on my list, *Paratemnoides insubidus*, is very close to *P. ellingseni*. Its genitalia are almost identical, but it differs in the external morphology by having a patella that is wider seen in lateral view, having a shape like the seed bulb of a poppy. The trochanter, however, has the same pointed bulge dorsally as *P. ellingseni*. Considering the differences in this group, I must conclude that this genus is polyphyletic with *P. ellingseni* and *P. insubidus* forming a separate group that stands apart from the others.

Titanatemnus species (Figs. 11–14): The species examined in this genus seem to constitute a fairly homogenous group, perhaps with *T. palmquisti* being the most divergent. All other species have a pronounced bipartite ventral diverticulum, a lobed or rounded projection on the longitudinal fold, a significant extention of the medial diverticulae and a characteristic form of the ejaculatory canal atrium. *Titanatemnus natalensis* is very close to *T. gigas* (the type species) in genital configuration, with the extension of the medial diverticulae being less protruding and the lateral lip of the lateral apodeme slightly straighter, more like in *T. sjoestedti*. However *T. palmquisti* is aberrant in having a less cleft bilobation of the ventral diverticulum, a more pointed projection on the longitudinal folds and slightly more transversely directed lateral lips. The overall configuration lies somewhere between the *Titanatemnus* and *Cyclatemnus* type. In the light of this it is interesting to note that Mahnert (1983) has pointed to some affinites between this species and *Cyclatemnus fallax* and *C. burgeoni*.

In conclusion, when considering the configuration of the male genitalia within existing genera, it is obvious that the diagnostic characters currently used have led to misplacements and to systematic groupings that do not reflect true phylogenetic relationship inside the family. Admittedly, the external morphogy has only occasionally been taken into consideration in the present discussion and has not been treated in a systematic manner. A more meticulous treatment of these characters in a cladistic analysis, together with those of genitalia, should provide a clearer understanding of relationships between the genera.

ACKNOWLEDGMENTS

I wish to thank Dr. Mark Judson, Muséum national d'Histoire naturelle, Paris, Dr. Volker Mahnert, Muséum d'Histoire naturelle, Geneva, Dr. Mark Harvey, Western Australian Museum, Perth and Dr. Gerald Legg, Booth Museum of Natural History, Brighton for giving me very valuable criticism and advice. What this paper has gained in quality is certainly due to their efforts, the remaining weaknesses are of course my responsibility. Furthermore, I wish to thank all the persons at the museums stated earlier who kindly lent me specimens for investigation and generously and patiently extended loans, often several times, when necessary.

LITERATURE CITED

Balzan, L. 1888. Chornetidae nonnullae Sud-Americanae. Asuncion, Paraguay. III.

Balzan, L. 1890. Revisione dei Pseudoscorpioni del Bacino dei Fiumi Paranà e Paraguay nell'America Meridionale. Annali del Museo Civico di Storia Naturale di Genova (2a) 9:401–454.

Balzan, L. 1892. Voyage de M. E. Simon au Venezuela (Décembre 1887–Avril 1888). Arachnides. Chernetes (Pseudoscorpiones). Annales de la Société Entomologique de France 60:497–552.

Beier, M. 1932a. Revision der Atemnidae (Pseudoscorpionidea). Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere 62:547–610.

Beier, M. 1932b. Pseudoscorpionidea II. Subord. C. Cheliferinea. Tierreich 58:i–xxi, 1–294.

Beier, M. 1972. Pseudoscorpionidea aus dem Parc national Garamba. Exploration Parc National de la Garamba, Mission H. de Saeger 56:2–19.

Beier, M. 1979. Neue afrikanische Pseudoskorpione aus dem Museé Royal de l'Afrique Centrale in Tervuren. Revue de Zoologie Africaine 93(1): 101–113.

Chamberlin, J.C. 1931. The arachnid order Chelonethida. Stanford University Publications, Biological Sciences 7(1):1–284.

Chamberlin, J.C. 1939. New and little-known false scorpions from the Marquesas Islands. Bulletin of the Bernice P. Bishop Museum 142:207–215.

Chamberlin, J.C. 1947. Three new species of false scorpions from the islands of Guam. Occasional Papers of the Bernice P. Bishop Museum 18(20): 305–316.

Dashdamirov, S. & W. Schawaller. 1993. Pseudoscorpions from Middle Asia, Part 3 (Arachnida: Pseudoscorpiones). Stuttgarter Beiträge zur Naturkunde, Ser. A (Biologie) 497:1–16.

Dumitresco, M. & T. Orghidan. 1969. Sur deux espèces nouvelles de Pseudoscorpions (Arachnides) lithoclasicoles de Roumanie: *Diplotemnus vachoni* (Atemnidae) et *Dactylochelifer marlausicolus*. Bulletin du Muséum National d'Histoire Naturelle, Paris (2) 41:675–687.

Dumitresco, M. & T. Orghidan. 1970. Cycle du développement de *Diplotemnus vachoni* Dumitresco et Orghidan, 1969, appartenant à la nouvelle famille des Miratemnidae (Arachnides, Pseudoscorpions). Bulletin du Muséum National d'Histoire Naturelle, Paris (2) 41(supplément 1): 128–134.

Ellingsen, E. 1906. Report on the pseudoscorpions of the Guinea Coast (Africa) collected by Leonardo Fea. Annali del Museo Civico di Storia Naturale di Genova (3) 2:243–265

Ellingsen, E. 1908. Pseudoscorpiones. In Strand, E., Arachniden aus Madagaskar. Zoologische Jahrbücher, Systematik (Ökologie), Geographie und Biologie 26:487–488.

Harvey, M.S. 1988. Pseudoscorpions from the Krakatau Islands and adjacent regions, Indonesia (Chelicerata: Pseudoscorpionida). Memoirs of the Museum of Victoria 49:309–353.

Harvey, M.S. 1991. Catalogue of the Pseudoscorpionida. Manchester University Press, Manchester.

Harvey, M.S. 1992. The phylogeny and classification of the Pseudoscorpionida (Chelicerata: Arachnida). Invertebrate Taxonomy 6:1373–1435.

Heurtault, J. 1970. Pseudoscorpions du Tibesti (Tchad). III. Miratemnidae et Chernetidae. Bulletin du Muséum National d'Histoire Naturelle, Paris (2) 42:192–200.

Heurtault, J. 1971. Chambre génitale, armature génitale et caractères sexuels secondaires chez quelques espèces de Pseudoscorpions (Arachnides) du genre *Withius*. Bulletin du Muséum National d'Histoire Naturelle, Paris (2) 42:1037–1053.

Legg, G. 1974. A generalised account of the male genitalia and associated glands of pseudoscorpions (Arachnida). Bulletin of the British Arachnological Society 3:66–74.

Legg, G. & R.E. Jones. 1988. Pseudoscorpions (Arthropoda; Arachnida). Synopsis of the British Fauna (New Series) 40:1–159. The Linnean Society of London.

Mahnert, V. 1983. Die Pseudoskorpione (Arachnida) Kenyas VII. Miratemnidae und Atemnidae. Revue Suisse de Zoologie 90:357–398.

Proctor, H.C. 1993. Mating biology resolves trichotomy for cheliferoid pseudoscorpions (Pseudoscorpionida, Cheliferoidea). Journal of Arachnology 21:156–158.

Schawaller, W. 1994. Pseudoscorpione aus Thailand (Arachnida: Pseudoscorpiones). Revue Suisse de Zoologie 101(3):725–759.

Thorell, T. 1889. XXI. Aracnidi Artrogastri Birmani raccolti da L. Fea nel 1885–1887. Ordo Chelonethi (In: Viaggio di Leonardo Fea in Birmani e Regione Vicine). Annali del Museo Civico di Storia Naturale di Genova (2) 7:591–607.

Tullgren, A. 1907. Zur Kenntnis aussereuropäischen Chelonethiden des Naturhistorischen Museums in Hamburg. Mitteilungen aus dem Naturhistorischen Museum in Hamburg 24:21–75.

Vachon, M. 1938a. Recherches anatomiques et biologiques sur la réproduction et le développement des Pseudoscorpions. Annales des Sciences Naturelles, Zoologie (11) 1:1–207.

Vachon, M. 1938b. Voyage en A. O. F. de L. Berland et J. Millot. IV. Pseudoscorpions. Première note. Atemnidae. Bulletin de la Société Zoologique de France 63:304–315.

Vachon, M. 1952. La reserve naturelle intégrale du

Mt. Nimba. II. Pseudoscorpions. Mémoires de l'Institut Francais d'Afrique Noire 19:17–43.

Weygoldt, P. 1970. Vergleichende Untersuchungen zur Fortpflanzungsbiologie der Pseudoscorpione II. Zeitschrift für Zoologische Systematik und Evolutionforschung 8:241–259.

With, C.J. 1906. The Danish Expedition to Siam 1899–1900. III. Chelonethi. An account of the Indian false-scorpions together with studies on the anatomy and classification of the order. Det Kongelige Danske Videnskabs Selskabs Skrifter 7(III):1–214.

With, C.J. 1908. An account of the South-American Cheliferinae in the collections of the British and the Copenhagen Museums. Transactions of the Zoological Society of London 18:217–340.

Manuscript received 7 February 2003, revised 3 February 2004.

2005. The Journal of Arachnology 33:663–669

EXTREMELY SHORT COPULATIONS DO NOT AFFECT HATCHING SUCCESS IN *ARGIOPE BRUENNICHI* (ARANEAE, ARANEIDAE)

Jutta M. Schneider and **Lutz Fromhage**: Biozentrum Grindel, Martin-Luther-King Platz 3, 28146 Hamburg, Germany

Gabriele Uhl: Institut für Zoologie, Abt. Neuroethologie, Endenicher Allee 11–13, 53115 Bonn, Germany

ABSTRACT. Females of the orb-weaving spider *Argiope bruennichi* are very cannibalistic and regularly terminate copulations by aggressively attacking the male. Few males survive mating and they escape only if they mate no longer than 8 seconds on average. We speculated that the brief copulations of surviving males will not result in complete fertilization of all of a female's eggs and that multiple mating is necessary to compensate for that. Surprisingly, we found no difference in the proportion of hatched young in clutches of females that were experimentally assigned to mate once or twice. Even females that mated with one male for less than 10 seconds produced clutches with hatching rates no different than treatments with two matings. The question remains why males risk their lives by prolonging copulation duration. Possible causes and functions in the context of sexual selection are discussed.

Keywords: Sexual cannibalism, sexual conflict, orb-weaving spiders, mating behavior

Theory suggests that male fitness increases with the number of females with whom they mate (Bateman 1948). However, it is less clear why females mate with more than one male in many animal species. A considerable body of recent literature investigates the question why females mate multiply and which kind of direct (Arnqvist & Nilsson 2000) or indirect (Jennions & Petrie 2000) benefits could be responsible. One such potential benefit is the avoidance of unfertilized eggs due to sperm limitation (Arnqvist & Nilsson 2000). A consequence of multiple mating by females is that the sperm of different males competes for the fertilization of a female's eggs. Sperm competition selects for male strategies that enhance the relative success of males (Elgar 1998; Simmons 2001). The duration of copulation is an important trait in this respect because it may, for example, determine the quantity of sperm transferred, aid removal of sperm from previous males, increase the probability that females will store and use the sperm or, for long copulations decrease the opportunities for females to copulation with another male. Males are thus under strong selection to achieve an optimal duration of copulation. However, mating can be costly to females. For example males can manipulate female reproductive behavior (Chapman et al. 2003) or even cause direct physical harm to females (Crudgington & Siva-Jothy 2000). In these cases, we expect a sexual conflict over the duration of copulation where females will often attempt to end copulation earlier than the males (Stockley 1997).

In spiders, the duration of copulation varies largely across taxa (Elgar 1995; Stratton et al. 1996) and is relatively short in the orb-web spiders, particularly in the genus *Argiope* Audouin 1826. Orb-weavers show a high frequency of post-mating sexual cannibalism and in a comparative analysis, Elgar (1995) found that within the Araneidae, sexually cannibalistic genera have shorter copulation durations than other taxa.

From the female perspective, the timing of cannibalism during mating seems an ideal instrument to control the duration of copulation. In *Argiope keyserlingi* Karsch 1878, females can adjust the relative paternity of two males by selectively timing copulation duration through attacking the male (Elgar et al. 2000). It was therefore suggested that cannibalism

evolved under sexual conflict over the control of mating (Elgar et al. 2000; Schneider & Elgar 2001; Schneider et al. 2000).

In *Argiope bruennichi* Scopoli 1772 as in other *Argiope* species, the female often terminates copulation aggressively by attacking the male. Most such cannibalistic attacks are fatal to the male. Unlike some other spiders (Forster 1992; Andrade 1996), *Argiope* males will try to escape, at least after their first copulation (Sasaki & Iwahashi 1995; Elgar et al. 2000). Surviving males usually lose at least one of their legs in the attempt to escape the fangs of the female (Fromhage et al. 2003). An experimental study showed that surviving males copulated less than 10 seconds while cannibalized males remained attached to the females up to 8 times longer (Fromhage et al. 2003). If the brief copulations with surviving males are not sufficient to allow sperm transfer, what appears to be post-mating cannibalism will be classified more appropriately as pre-mating cannibalism.

Here, we explore this possibility by measuring hatching success in relation to sexual cannibalism and in relation to the number and duration of copulations. We allowed females to mate with one or with two males and compared hatching success of three successive egg sacs. We expected that a single short copulation would not result in complete fertilization of a female's eggs. In double mating trials we expected that females which received a very brief first copulation would compensate for this by acquiring an increased sperm supply from a following male.

METHODS

Subadult females (80) and adult males (about 120) of *A. bruennichi* were collected in July and August 2002, from dense populations in patches of grassland within the city of Bonn, Germany. Voucher specimens are deposited at the Museum Alexander Koenig in Bonn, Germany. Females were housed in individual plastic cups (400 ml) where they were watered 6 days per week and fed about 3–4 *Calliphora* sp. flies every 2–3 days. Adult females were housed in separate Perspex frames (30 cm x 30 cm x 6 cm), where they built typical orb-webs. After mating, they were retransferred to plastic cups where they were checked for egg sacs 6 days per week. Egg sacs were stored in individual plastic vials and preserved in alcohol after 26–29 days of incubation at 25 °C. Hatchlings and undeveloped eggs were subsequently counted under the microscope. Clutch size was the combined number of the number of hatchlings and the number of undeveloped eggs. After the natural death of a female, we used calipers to take the tibia-patella length of a first foreleg as a measure of its fixed body size. We randomized the choice of left or right leg but used the intact leg if one of the front legs was obviously shorter than the other or the second leg. We used body mass divided by tibia-patella length as an estimate for condition, ensuring the requirement that the relation between these parameters was largely isometric within the range of our data. Since females were weighed after their final molt and after mating, we could quantify their mass gain. In order to correct this mass difference for body size, we used condition. We obtained condition at maturity as mass at maturity divided by fixed body size, and condition at mating as mass at mating divided by fixed body size (=tibia-patella length). Males were of unknown mating status since they were collected in the field as adults. The majority of these males possessed all eight legs. Given the high mortality rate during copulation and a high probability of survivors to have lost at least one leg (Fromhage et al. 2003) and the observation that each pedipalp is used only once (unpub. data), we assume that most of these males were virgin. In the lab, they were maintained in individual cups (150 ml) on a diet of *Drosophila*. Shortly before mating, each male was weighed and the tibia-patella length of a foreleg was measured while he was immobilized by covering him with plastic film.

Females were randomly assigned to one of two different mating treatments: they were either presented with a single male that was allowed one insertion or with two males in succession each allowed a single insertion. There were 38 females in each of the two treatments. The mean duration of the 1st copulation did not differ between treatments (Mann-Whitney-U-Test, $Z = -1.48$, $P = 0.14$). Matings were staged by placing a male near a support thread of the females' orb-web. When the male entered the web, the female would typically assume a distinctive posture with its body lifted from the web, often swaying slightly. The male then traversed the web to

the hub and ran over the female a few times before he inserted one of his pedipalps. Time to copulation was measured with a stopwatch from the moment the male entered the web until the beginning of copulation. We measured copulation duration from pedipalp insertion until withdrawal.

Data analyses were carried out using JMP 4.02. Not all data were available for each mating trial and therefore sample sizes may differ between analyses. To fit a normal distribution, copulation duration, total copulation duration and male mass were log-transformed when parametric statistics were performed. We used nonparametric statistics where normally distributed residuals could not be obtained, or where variances were unequal. The use of Spearman correlations is indicated by the symbol r_s for the correlation coefficient, the use of Chi-square tests by indication of χ^2_1.

RESULTS

Clutch size and hatching success.—Mated females in the laboratory (all treatments combined) laid an average of 2.1 ± 0.2 clutches (mean ± SE, $n = 76$). The average clutch size was 170.7 ± 5.2 (clutch 1–3, $n = 133$) and did not differ significantly between 1st, 2nd and 3rd clutches (Oneway-Anova: $F_{2, 130} = 2.01$, $P = 0.14$). If clutch sizes of successive clutches are compared considering individual females as block effects, we also found no significant difference (Oneway-Anova: $F_{2, 68} = 2.68$, $P = 0.076$).

The proportion of hatched eggs differed significantly between successive clutches ($\chi^2_2 = 23.84$, $P < 0.0001$). Pairwise comparisons of the means using Dunns method for nonparametric comparisons with unequal sample sizes (Zar 1999) revealed a significantly lower percentage of hatched eggs in third clutches (0.42 ± 0.06, $n = 35$) than in first (0.60 ± 0.05, $n = 53$) and second (0.73 ± 0.05, $n = 45$) clutches ($P < 0.05$). Egg sacs collected from the habitat of the source population contained an average of 271.7 ± 20.0 eggs with a proportion of hatched eggs of 0.98 ± 0.02 ($n = 20$).

Size of the first clutch was significantly related to female fixed body size ($r_s = 0.54$, $P < 0.001$, $n = 55$), female condition at mating ($r_s = 0.38$, $P = 0.021$, $n = 36$), but not with female condition at maturation ($r_s = 0.25$, $P = 0.11$, $n = 43$).

None of these female body parameters was correlated with the proportion of hatched eggs in the 1st clutch (female fixed adult size (tibia-patella length): $r_s = -0.08$, $P = 0.6$, $n = 55$; female mass at maturity: $r_s = -0.11$, $P = 0.44$; female condition at maturation: $r_s = -0.07$, $P = 0.67$, $n = 43$; female condition at mating: $r_s = -0.15$, $P = 0.41$, $n = 36$). Clutch size and hatching success were not correlated for 1st and 3rd clutches although we found a positive correlation for 2nd clutches (1st egg sac: $r_s = 0.21$, $P = 0.14$; 2nd egg sac: $r_s = 0.45$, $P = 0.002$; 3rd egg sac: $r_s = 0.22$, $P = 0.20$).

Sperm availability and copulation duration.—There were no indications that sperm availability is a limiting factor of female reproductive success. Neither the proportion of eggs hatched nor the number of hatchlings significantly depended on the number of matings that a female experienced (number of matings vs. % hatched eggs: 1st egg sac: $\chi^2_1 = 0.22$, $P = 0.64$, 2nd egg sac: $\chi^2_1 = 1.86$, $P = 0.17$, 3rd egg sac: $\chi^2_1 = 1.98$, $P = 0.16$ (Fig. 1); number of matings vs. number of hatchlings: 1st egg sac: $\chi^2_1 = 0.12$, $P = 0.73$, 2nd egg sac: $\chi^2_1 = 0.02$, $P = 0.89$, 3rd egg sac: $\chi^2_1 = 2.78$, $P = 0.10$).

Similarly, the total duration of copulation that a female experienced was not correlated with the absolute number of hatchlings nor with relative hatching success of clutches: non-parametric correlations of total copulation duration vs. % hatched eggs: 1st egg sac: $r_s = -0.14$, $P = 0.32$, $n = 53$ (Fig. 2), 2nd egg sac: $r_s = 0.01$, $P = 0.94$, $n = 45$, 3rd egg sac: $r_s = -0.04$, $P = 0.83$, $n = 35$; total copulation duration vs. number of hatchlings: 1st egg sac: $r_s = -0.03$, $P = 0.86$, $n = 55$, 2nd egg sac: $r_s = 0.25$, $P = 0.10$, $n = 48$, 3rd egg sac: $r_s = 0.03$, $P = 0.85$, $n = 36$).

Copulation duration of cannibalistic matings was much longer than in copulations with surviving males, as reported elsewhere (Fromhage et al., 2003). While cannibalized males mated for a median of 23s (upper quartile = 35.9s, lower quartile = 10.27s, $n = 148$), survivors copulated for a median of only 7.8s (upper quartile = 11.5s, lower quartile = 6s, $n = 40$) (median is given because the data are not normally distributed).

Regarding cannibalistic first matings (with two outliers excluded to obtain a normal distribution), the duration of copulation was pos-

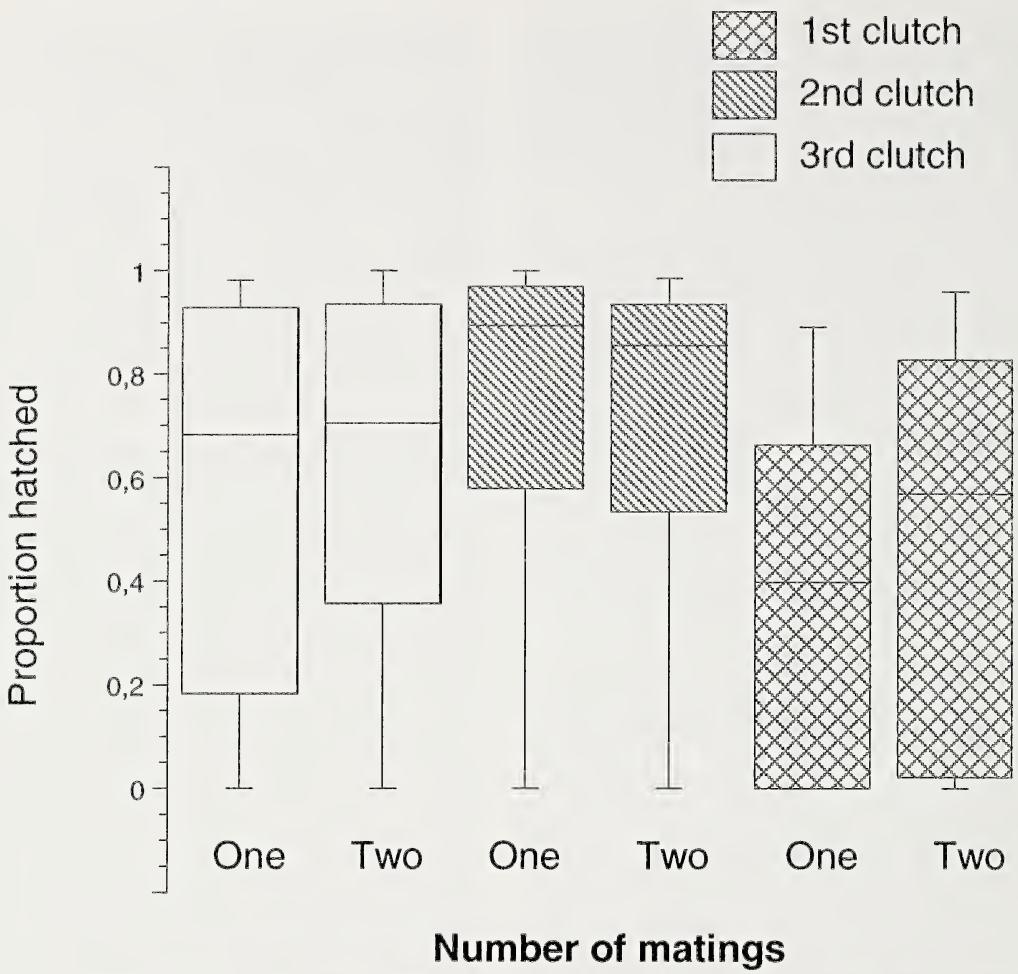


Figure 1.—Proportion of young hatched in three successive egg sacs of females that mated with one or two males. Box plots show median, interquartiles and range.

itively predicted by fixed male body size (linear regression: $r^2 = 0.09$, $P = 0.03$, $n = 58$) but not by male body mass ($r^2 = 0.04$, $P = 0.15$, $n = 59$) nor time to copulation (linear regression: $r^2 = 0.01$, $P = 0.61$, $n = 59$). In 25 cases, where females were cannibalistic towards both of her mates, the difference in body size of the males did not correlate with the difference in copulation duration ($r_s = -0.1$, $P = 0.58$).

First and second matings of the same females revealed no significant difference regarding copulation duration when compared with the Wilcoxon signed rank test for matched pairs ($Z = -0.43$, $P = 0.68$, $n = 38$). Females that received short non-cannibalistic 1st matings ($N = 7$) did not copulate longer with the 2nd male than 31 females that cannibalized their 1st mate (mean ± SE, cannibalistic: 20.45 ± 4.1, non-cannibalistic: 25.86 ± 8.58 ; t-test: $t = 0.57$, $P = 0.57$). In addition, females whose first mating was shorter than 10s (independent of cannibalism) did not mate longer with a 2nd male than females with a longer 1st copulation (22.37s ± 3.5, $n = 26$ long vs 19.45s ± 8.9, $n = 12$ short copulations; Wilcoxon Test: $Z = -1.13$, $P = 0.25$).

Large females produced more eggs, but female size did not influence the duration of her 1st ($r_s = 0.013$, $P = 0.9$) or 2nd ($r_s = 0.29$, $P = 0.1$) copulation.

DISCUSSION

Argiope bruennichi females are very cannibalistic and aggressively attack most males

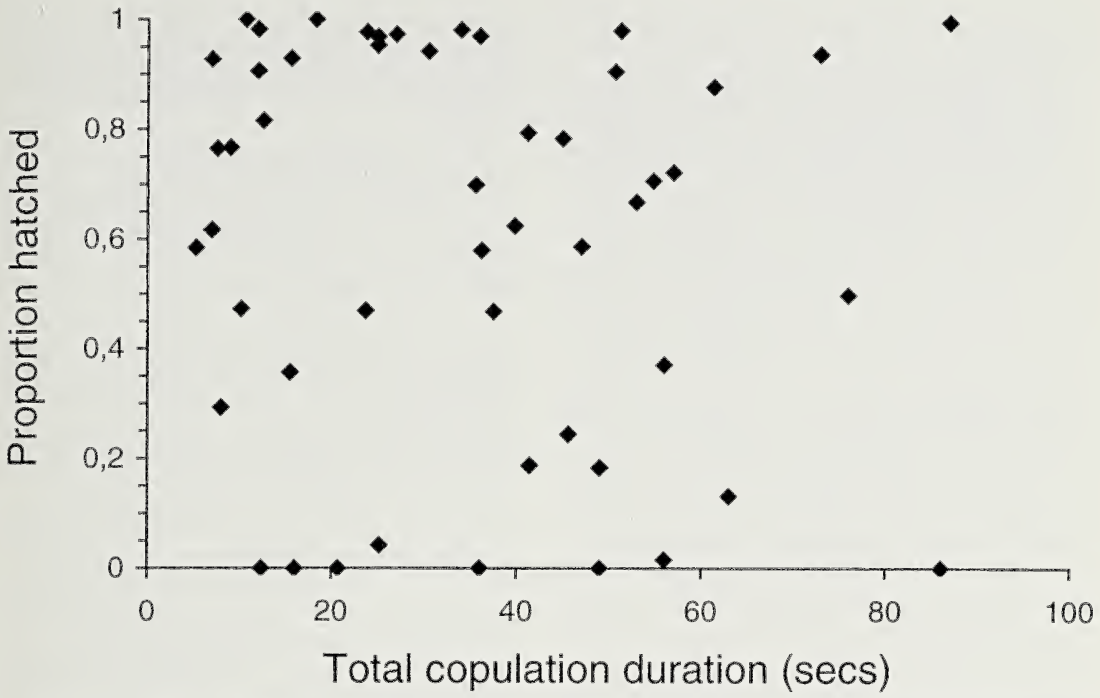


Figure 2.—The proportion of young hatched in the 1st clutch as a function of the total duration of copulation a female experienced.

that mate with them. In 80% of all cases, the female kills and consumes the male, thereby terminating copulation. The duration of copulation strongly depends on the fate of the male, with copulations of survivors being extremely short (median of 8 seconds). We speculated that sperm transfer in extremely brief matings would not be sufficient to fertilize all eggs in a female's successive clutches.

To our surprise, we did not find any relationship between the duration of copulation and hatching success. Eggs of females who copulated once for only 5 seconds achieved hatching rates comparable to females who mated twice, and/or experienced those with much longer copulations. We did not detect any predictor of hatching success: hatching success was not related to female body size and mass nor to the size of the clutch. However, we found a positive correlation between clutch size and hatching rate for 2nd clutches. As known for many spider species (Marshall & Gittleman 1994), clutch size in *A. bruennichi* is a function of female size and condition at mating. This may suggest that large females with large clutches achieve higher fertilization rates because males mate longer and/or are more willing to risk their lives when mating with more fecund females. However, female size, mass, and condition were not correlated with the duration of copulation (Fromhage et al. 2003).

Hatching success in the laboratory was lower than in the field, which is likely a consequence of the conditions that we provided. However, conditions were controlled and the same for all the females. It is therefore unlikely that our results are affected by the generally low hatching success. A factor that we cannot exclude is that females in the field mated with many more than two males and that more males are necessary to guarantee complete fertilization. However, in 18 1st clutches we found a hatching success above 90% and among these females, 50% mated once, one female for only 7 seconds.

Although 3rd clutches had lower hatching rates than 1st clutches, this is not explained by the mating experience of the female. Fertilization rates may simply go down with time, perhaps through loss or aging of stored sperm cells. In this case, polyandry in *A. bruennichi* Scopoli 1772 may serve as a strategy to re-

duce this cost through repeated transfer of viable sperm.

Our results suggest that males can transfer enough sperm within a few seconds to ensure complete fertilization. Why then would males mate longer and risk their lives? Given the high risk of cannibalism for males that mate longer than a few seconds, a benefit of prolonged copulation is predicted that may offset the costs of losing all future mating chances. There are a number of possibilities that need to be investigated in future research projects. Firstly, sperm transfer may continue and even though additional sperm is not required for the purpose of fertilization, increased sperm numbers may be advantageous in sperm competition (Simmons 2001). This is likely if the outcome of sperm competition is determined by the relative quantity of sperm of rival males much like in a fair raffle (Parker 1990; Wedell et al. 2002). Such mechanisms have been demonstrated in insects (e.g. Dickinson 1986; Keller & Passera 1992). In a congener of our study species, *A. keyserlingi*, relative copulation duration of two competing males determines their relative paternity (Elgar et al. 2000), and similar relationships have been detected in *Nephila edulis* Labillardiere 1799 (Schneider et al. 2001) and *Pholcus phalangioides* Fuesslin 1775 (Schäfer & Uhl 2002). However, in none of these studies has it been determined whether the transfer of sperm was responsible for the advantage in sperm competition. In fact, the linear relationship between copulation duration and sperm transfer that has been demonstrated for many insects may not be valid for spiders. Several studies on spiders found no such relationship (Bukowski & Christenson 1997; Christenson & Cohn 1988; Willey Robertson & Adler 1994, Uhl unpubl. data), indicating that large parts of spider copulatory behavior serve functions other than sperm release (Eberhard 1994, 1996).

Given that under sperm competition copulation duration influences relative paternity, males will have an interest to prolong copulation while females may benefit by selectively terminating copulation. If copulation duration is largely under female control, males will best serve their interest by speeding up the mating procedure. This in turn will feed back on the female behavior. A conflict over copulation duration may therefore drive an antagonistic co-evolution, with copulations becoming shorter and shorter until an absolute minimal duration sets a limit to the evolutionary race.

ACKNOWLEDGMENTS

This project was funded by a grant of the Deutsche Forschungsgemeinschaft to JMS Schn561/5). We are grateful to the city council of Bonn for their support.

LITERATURE CITED

Andrade, M.B.C. 1996. Sexual selection for male sacrifice in the Australian redback spider. Science 271:70–72.

Arnqvist, G. & T. Nilsson. 2000. The evolution of polyandry: multiple mating and female fitness in insects. Animal Behaviour 60:145–164.

Bateman, A.J. 1948. Intra-sexual selection in *Drosophila*. Heredity 2:349–368.

Bukowski, T. & T. Christenson. 1997. Determinants of sperm release and storage in a spiny orbweaving spider. Animal Behaviour 53:381–395.

Chapman, T., G. Arnqvist, J. Bangham, & L. Rowe. 2003. Sexual conflict. Trends in Ecology and Evolution 18:41–47.

Christenson, T. & J. Cohn. 1988. Male advantage for egg fertilization in the golden orbweaving spider, *Nephila clavipes*. Journal of Comparative Psychology 102:312–318.

Crudgington, H.S. & M.T. Siva-Jothy. 2000. Genital damage, kicking and early death. Nature 407: 855–856.

Dickinson, J.L. 1986. Prolonged mating in the milkweed leaf beetle *Labidomera clivicollis clivicollis* (Coleoptera: Chrysomelidae): a test of the sperm-loading hypothesis. Behavioural Ecology and Sociobiology 18:331–338.

Eberhard, W.G. 1994. Evidence for widespread courtship during copulation in 131 species of insects and spiders, and implications for cryptic female choice. Evolution 48:711–733.

Eberhard, W.G. 1996. Female Control: Sexual Selection by Cryptic Female Choice. Princeton University Press, Princeton, New Jersey.

Elgar, M.A. 1995. The duration of copulation in spiders: comparative patterns. Records of the Western Australian Museum Supplement No. 52: 1–11.

Elgar, M.A. 1998. Sperm competition and sexual selection in spiders and other arachnids. Pp. 307–332. *In* Birkhead, T. R. & A. P. Møller (eds.) Sperm competition and sexual selection. London, Academic Press.

Elgar, M.A., J.M. Schneider, & M.E. Herberstein. 2000. Female control of paternity in the sexually cannibalistic spider *Argiope keyserlingi*. Proceedings of the Royal Society London Series B 267:2439–2443.

Forster, L.M. 1992. The stereotyped behaviour of sexual cannibalism in *Latrodectus hasselti* Thorell (Araneae: Theridiidae): the Australian redback spider. Australian Journal of Zoology 40:1–11.

Fromhage, L., G. Uhl, & J.M. Schneider. 2003. Fitness consequences of sexual cannibalism in female *Argiope bruennichi*. Behavioural Ecology and Sociobiology 55:60–64.

Jennions, M.D. & M. Petrie. 2000. Why do females mate multiply? A review of the genetic benefits. Biological Reviews 75:21–64.

Keller, L. & L. Passera. 1992. Mating system, optimal number of matings, and sperm transfer in the Argentine ant *Iridomyrmex humilis*. Behavioural Ecology and Sociobiology 31:359–366.

Marshall, S.D. & J.L. Gittleman. 1994. Clutch size in spiders: is more better? Functional Ecology 8: 118–124.

Parker, G.A. 1990. Sperm competition games: Raffles and roles. Proceedings of the Royal Society London Series B: 242:120–126.

Sasaki, T. & O. Iwahashi. 1995. Sexual cannibalism in an orb-weaving spider *Argiope aemula*. Animal Behaviour 49:1119–1121.

Schäfer, M.A. & G. Uhl. 2002. Determinants of paternity success in the cellar spider *Pholcus phalangioides* (Araneae: Pholcidae): the role of male and female mating behaviour. Behavioural Ecology and Sociobiology 51:368–377.

Schneider, J.M. & M.A. Elgar. 2001. Sexual cannibalism and sperm competition in the golden orb-web spider *Nephila plumipes* (Araneoidea): female and male perspectives. Behavioral Ecology 12:547–552

Schneider, J.M., M.E. Herberstein, F.C. De Crespigny, S. Ramamurthy, & M.A. Elgar. 2000. Sperm competition and small size advantage for males of the golden orb-web spider *Nephila edulis*. Journal of Evolutionary Biology 13:939–946

Schneider, J.M., M.L. Thomas, & M.A. Elgar. 2001. Ectomised conductors in the golden orb-web spider *Nephila plumipes* (Araneoidea): a male adaptation to sexual conflict? Behavioural Ecology and Sociobiology 49:410–415

Simmons, L.W. 2001. Sperm Competition and Its Evolutionary Consequences in the Insects. Princeton University Press, Princeton and Oxford.

Stockley, P. 1997. Sexual conflict resulting from adaptations to sperm competition. Trends in Ecology and Evolution 12:154–159.

Stratton, G.E., E.A. Hebets, P.R. Miller, & G.L. Miller. 1996. Patterns and duration of copulation in wolf spiders (Araneae, Lycosidae). Journal of Arachnology 24:186–200.

Wedell, N., M.J.G. Gage, & G.A. Parker. 2002. Sperm competition, male prudence and sperm limited females. Trends in Ecology and Evolution 17:313–320.

Willey Robertson, M. & P.H. Adler. 1994. Mating behavior of *Florinda coccinea* (Hentz) (Araneae: Linyphiidae). Journal of Insect Behavior 7:313–326.

Zar, J.H. 1999. Biostatistical Analysis, 4th ed. Prentice Hall, New Jersey.

Manuscript received 19 May 2003, revised 12 December 2003.

2005. The Journal of Arachnology 33:670–680

PARAMETERS AFFECTING FECUNDITY OF *LOXOSCELES INTERMEDIA* MELLO-LEITÃO 1934 (ARANEAE, SICARIIDAE)

Marta L. Fischer: Departamento de Biologia, Centro de Ciências Biológicas e da Saúde, Pontifícia Universidade Católica do Paraná. Núcleo de Estudos do Comportamento. Av. Silva Jardim, 1664/1101–CEP 80250–200–Curitiba, Paraná, Brazil. E-mail: nephilla@terra.com.br

João Vasconcellos-Neto: Departamento de Zoologia, Instituto de Biologia–Universidade Estadual de Campinas–UNICAMP–C.P. 6109–Campinas, São Paulo, Brazil. CEP 13083–970, Brazil.

ABSTRACT. In this study, the process of egg sac construction and the factors that determine fecundity in the spider *Loxosceles intermedia* were analyzed by comparing lab-reared females that had mated only once (n = 180 ovipositions) and females with unknown reproductive histories (n = 76 ovipositions). Among females known to have mated only once (n = 84), the number of viable eggs correlated positively with the duration of mating and with the age of the female at the time of fertilization and decreased significantly with successive ovipositions. In females with unknown (n = 36) reproductive histories, up to three fertile egg sacs were obtained from the same female with a third oviposition being observed only once. Oviposition was more frequent among larger females than smaller females. Among the reproductive variables evaluated, there were correlations between the number of eggs and the weight of the female spiders. More fertile eggs were laid by females with unknown reproductive histories than by females that mated only once. The existence of more stable environmental conditions, abundant food, and multiple fertilizations are probable factors which favor greater fertility of *L. intermedia* in urban Curitiba, located in southern Brazil, and can partly explain the success of this species in occupying this ecological niche.

Keywords: Ovipositions, fertility, reproduction, mating success

Spider egg sacs protect developing eggs against abiotic (temperature, luminosity and relative humidity of the air) and biotic (predators and parasites) factors. Egg sac construction is a rigidly controlled and programmed behavior (Foelix 1996). Fecundity is often defined as the number of eggs or offspring an animal produces during each reproductive cycle (Begon et al. 1990). Various studies have examined fecundity in spiders (Cooke 1965; Levy 1970; Muniappan & Chada 1970) and, according to Downes (1985), the estimates of fecundity should include the number of emerged spiderlings and all of the individuals in different stages of development which belong to the same ovisac, including undeveloped eggs. Inter- and intraspecific variation in fecundity have been attributed to factors such as foraging success (Figueira & Vasconcellos-Neto 1993), temperature and humidity (Downes 1988), and photoperiod (Miyashita 1987). In addition, individual variation in reproduction have been attributed to factors such as size, age and physiological state of the female (Turnbull 1962; Eberhard 1979; Capocasale et al. 1984; Costa & Capocasale 1984; Fritz & Morse 1985), energy investment (Hoffmaster 1982), parental care (Enders 1976; Christenson & Wenzl 1980; Krafft 1982; Opell 1984; Nuessly & Goeden 1984; Downes 1984; Fink 1986; Ruttan 1991), spermatic depletion (Jackson 1978) and reproductive tactics (Killebrew & Ford 1985). Quantitative and qualitative fertility studies have been done in the laboratory for some Araneae species (Christenson et al. 1979; Downes 1985, 1987; Gonzales 1989; Willey & Adler 1989; Suter 1990; Wheeler et al. 1990). For this study, in which we examined a variety of factors that may influence reproductive success in *Loxosceles*, we defined fecundity as the total reproductive effort of the female (including multiple clutches).

The genus *Loxosceles* is cosmopolitan and is frequently associated with human settlements where the physical and environmental conditions favor an increase in the spider populations. Despite the medical importance of many species of this genus and their synanthropic habits, only a few studies have examined fecundity in *Loxosceles* species. These studies recorded only the number of eggs for *L. rufipes* (Lucas 1834) (Delgado 1966), *L. reclusa* Gertsch & Mulaik 1940 (Hite et al. 1966; Horner & Stewart 1967), *L. laeta* (Nicolet 1849) (Galiano 1967; Galiano & Hall 1973), *L. gaucho* Gertsch 1967 (Bücherl 1961; Rinaldi et al. 1997) and *L. hirsuta* Mello-Leitão 1931 (Fischer & Marques da Silva 2001). A comparative study of the number of eggs laid by *L. intermedia* and *L. laeta* was done by Andrade et al. (2000). Some of the studies (e.g., Bücherl 1961, Galiano 1967, Delgado 1966, Andrade et al. 2000) used spiders with unknown reproductive histories for characterization of fecundity of the respective species. The city of Curitiba (lat. 25°25′48″ S and long. 49°16′15″ W), capital of the Brazilian state of Paraná, has a large population of *Loxosceles* that is responsible for hundreds of bites each year, with the species being either: *L. intermedia* (90% of collections) or *L. laeta* (10% of collections) (Fischer 1994). The species *L. intermedia* has a restricted distribution to the south and southeast of Brazil. The wide distribution in the city and predominance of *L. intermedia* over *L. laeta* is related to many factors such as the more generalist habits of *L. intermedia*, as well as temperature and humidity favorable to *L. intermedia*. However, little is known of the factors which affect female fecundity in this species. In this study, we examined the reproductive potential and factors that affect the egg viability of *L. intermedia* females. These data will be useful for future experimental studies as well as management plans for the spiders to minimize spider bites. For the present study we compared the reproductive output of lab-reared females known to have mated once with virgin males (both males and females born and raised in laboratory, with known feeding history) with wild-caught adult females (number of mates, age and feeding history unknown).

METHODS

Egg sac construction.—Details of egg sac construction were observed in ten females chosen randomly, based on direct *ad libitum* observations.

Fecundity of females reared in the lab and mated once.—The fecundity of 84 females born, raised and mated once in the laboratory was evaluated. And, because we had detailed information about mating and maturation of these spiders, we looked at correlations of fecundity with duration of mating and age of the females. The spiders used in this study were kept in the laboratory from November 1994–December 1999. The spiders were maintained at ambient temperature 21.4 ± 2.3 °C, n = 19; range = 16.2–24.7 °C, air humidity 73.9 ± 11.4%, n = 19; range = 57.8–95.7 with lighting from 12:12 L:D cycle. The air temperature and relative humidity were monitored daily using a thermohydrograph. Young spiders were kept in 120 ml plastic containers (diameter of base 4.8 cm). All spiders were fed up to the 4th instar a standardized diet consisting of two larval and adult *Drosophila melanogaster* twice a week. After the 4th instar, the spiderlings were fed two *Tenebrio molitor* larvae twice a week and were placed in plastic containers (750 ml), lined with paper and kept in a laboratory in the Department of Zoology at Federal University of Paraná.

Once mature, the virgin females were each mated once with virgin males that had also been raised in laboratory. The mating of all the couples (n = 84) was induced during January–April 1996. The virgin females copulated with a single male and the duration of mating was the time that the embolous were inserted in the receptacles of the female, in a single encounter, typically 1289 ± 822 sec, n = 84; range = 73–3733 sec (Fischer & Vasconcellos-Neto 2000). Once the females had been mated and egg sacs constructed, the egg sacs were maintained with the female, at the site of oviposition, until spiderlings had emerged from the egg sacs. The relationships between the total number of eggs, the number of spiderlings, and the number of unhatched eggs versus the duration of mating and age of the female were examined.

Fecundity of wild-caught females with unknown reproductive histories.—Sixty four females were collected from residences in Curitiba and maintained in the laboratory until egg sacs were deposited. For this portion of the study we were most interested in cor-

relation in body size with fecundity. Mature spiders were collected from March–June 1994 and were maintained in individual containers. Temperature ranged from 18 °C to 29 °C and air humidity ranged from 63–88% humidity (details in Tables 4 & 5) from June 1994–November 1995. Temperature and humidity were measured for each individual. The egg sacs were laid between September 1994–March 1995. Thirty six of the 64 females constructed egg sacs. When the spiderlings emerged, they were weighed and fixed in 70% alcohol. In order to evaluate the influence of the weight of the female on her fecundity, the adult female was weighed to the nearest 0.1 mg an analytical electronic balance immediately after oviposition. In addition we measured cephalothorax area (length × width in mm) and the femur length of right leg I using a stereoscopic microscope with an ocular micrometer.

The number of hatched eggs was considered as an index of egg viability. Besides this index we also measured number of egg sacs, the total number of eggs, unhatched eggs, spiderlings, and the duration of incubation. We investigated correlations of these variables with female cephalothorax area (mm^2), female weight after oviposition, spiderling weight, average of natural temperature and relative humidity during the incubation period, and the time between consecutive ovipositions.

Statistical analysis.—The chi-squared test was used to assess differences between the number of females that laid eggs and those which did not, relative to their size. For this, the females were divided into two groups, i.e. those with a cephalothorax area less than or greater than 15 mm^2. Matrix correlations and multiple linear regression were used to examine the relationships between the parameters and the fecundity variables in females with unknown reproductive histories. Student's t test was used to compare the fecundity parameters between consecutive ovipositions when the variances were homogeneous and the Kruskal-Wallis (H) test was used when variances were not homogenous. The Mann-Whitney (U) test was used to compare the fecundity parameters between females with only one fertilization and those with unknown reproductive histories.

Male and female voucher specimens are deposited in Arachnological collection Dra. Vera Regina von Eicksted in the section of poisonous arthropods of the Imunologic Production and Research Center (SESA-PR), Piraquara, Paraná, Brazil.

RESULTS

Egg sac construction.—Egg sac construction began with the substrate being covered with thin silk threads. The female spider moved in circles with the abdomen directed towards the center of the web in order to join the radiating points. The female subsequently positioned herself vertically to begin egg laying. Approximately 30 min later, as soon as the egg mass became granular and the outline of each egg was visible, the spider started to construct the cover. The abdomen was placed over the eggs and threads were woven attaching the apex of the egg mass to the substrate. The abdomen was moved left to right and up and down, with the body being turned clockwise and counter-clockwise. Construction of the cover required about 4 h (n = 10). The first silk was similar to that of the substrate, with thicker threads being added through movements of the abdomen, legs and pedipalps. After finishing the construction, the female rested, and positioned herself over or next to the egg sac.

The egg sacs were disc-shaped and whitish, with an average diameter of 18.8 ± 1.1 mm (n = 25; range = 14–20). The egg mass had an average diameter of 9.9 ± 2.4 mm (n = 25; range = 8–15 mm) with a domed arrangement, and the eggs had an average diameter of 0.99 ± 0.01 mm (n = 25; range = 0.06–1).

Fecundity of females reared in the lab and mated once.—In this study, 180 egg sacs were obtained from 84 females from February 1996–February 1998. Three peaks of egg-laying were observed (October and December 1996, and March 1997) (Fig. 1).

Of the 84 mated females, 75 (89%) laid egg sacs. Of these, 61.1% (n = 110) were viable (spiderlings emerged); 21.1% (n = 38) were destroyed by the females (the eggs were eaten) before eclosion and in 17.8% (n = 32) the eggs dried out. In 41% (n = 75) of the spiders, only one egg sac was constructed. However many also laid between two and six egg sacs 31.1% (n = 56) laid two egg sacs, 22.2% (n = 40) laid three, 5% (n = 9) laid four, 1.6% (n = 3) laid five while one female laid a 6th

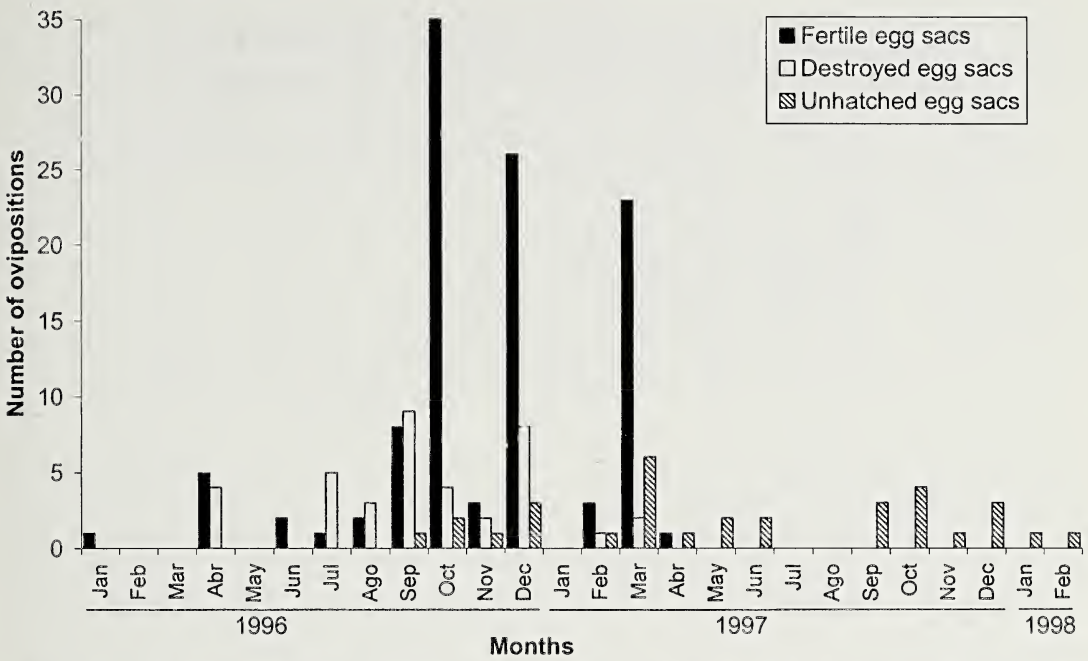


Figure 1.—Ovipositions (fertile, destroyed and non-ecloded eggs) of 75 *L. intermedia* females with known reproductive histories. The dates were obtained in the laboratory from February 1996–February 1998.

egg sac. Fertile egg sacs were not obtained in the 5th and 6th ovipositions (Table 1).

Fertile egg sacs had an average incubation time of 50.4 ± 11.7 days (n = 110; range = 30–106), an average number of spiderlings of 20.4 ± 21.1 (n = 110; range = 1–110) and an average number of non-ecloded eggs of 10.8 ± 13.8 (n = 108; range = 0–68). The average rate of egg viability was 70.2 ± 30.9% (n = 108; range = 4.2–100%). The results obtained in successive ovipositions are shown in Table 2. The number of viable eggs had a slight but significant positive correlation with the time spent in mating 1280 ± 836 sec (n = 75; range = 73–3757) (r^2 = 0.123; $P <$ 0.01) and with the age of the female spider at the time of mating 490 ± 39.9 days (n = 75; range = 245–551) (r^2 = 0.054; $P < 0.05$). The period of latency (period between two ovipositions) was not correlated with the total number of eggs in any of the ovipositions.

The number of viable eggs decreased in successive ovipositions (H = 10.3; $P < 0.01$), and the latency period increased from the 2nd oviposition onwards (H = 71.8; $P < 0.0001$). However, the length of incubation (H = 5.3; $P > 0.05$) and the number of unhatched eggs (H = 5.1; $P > 0.05$) were not significantly different.

Fecundity of wild-caught females with

Table 1.—Relative frequency of fertile, destroyed and dried egg sacs in successive ovipositions by female *L. intermedia* fertilized only once.

Egg sacs	1st oviposition	2nd oviposition	3rd oviposition	4th oviposition	5th oviposition	6th oviposition
Fertile	63.5% (n = 47)	66.7% (n = 36)	66.7% (n = 26)	11.1% (n = 1)	0	0
Destroyed	27% (n = 20)	24% (n = 13)	10.2% (n = 4)	0	33.3% (n = 1)	0
Dried	9.5% (n = 7)	9.3% (n = 5)	23.1% (n = 9)	88.9% (n = 8)	66.7% (n = 2)	100% (n = 1)

Table 2.—Fecundity parameters for *L. intermedia* females known to have mated only once. (The values are the mean ± s.e. with the sample size (*n*) and range in parentheses.)

Egg sacs	1st oviposition	2nd oviposition	3rd oviposition	4th oviposition	5th oviposition	6th oviposition
Incubation (days)	52.8 ± 14.5 (47; 33–106)	50.6 ± 10.3 (36; 30–80)	45.4 ± 4.7 (26; 31–53)	48 (*n* = 1)	—	—
Spiderlings	36.5 ± 21.8 (47; 1–110)	26.4 ± 22.5 (36; 2–77)	22 ± 14.2 (26; 1–59)	20 (*n* = 1)	—	—
Unhatched eggs	7.4 ± 8.8 (47; 0–42)	16.8 ± 19.4 (36; 0–68)	9.1 ± 9.4 (26; 0–35)	0 (*n* = 1)	—	—
Latency (days)	173.5 ± 81.8 (75; 25–656)	69.2 ± 45.6 (36; 11–238)	71.9 ± 50.6 (26; 10–212)	114.4 ± 66.1 (9; 32–239)	153 ± 107.1 (3; 75–203)	1142 (*n* = 1)

unknown reproductive histories.—From the 64 females collected, 36 constructed egg sacs (56.2%). Of these, 20 laid multiple egg sacs. A total of 76 egg sacs were observed between September 1994 and March 1995. Of these, 57 were viable and 19 were destroyed by the females (Fig. 2).

Oviposition was more frequent among larger females ($\chi^2 = 7.53$; $P < 0.01$; df = 1) than smaller females ($\chi^2 = 0.95$; $P > 0.05$; df = 1) (Fig. 3). In females with unknown reproductive histories, up to three fertile egg sacs were obtained from the same female with a third oviposition being observed only once. The average number of days between consecutive ovipositions was 68.8 ± 26 days (*n* = 20; range = 18–136 days). In our sample, 36.8% of the ovipositions showed 100% hatching, with the average percentage of non-viable eggs per egg sac being 17.5 ± 28.5% (*n* = 57; range = 0–97%). The average *L. intermedia* egg viability (proportion of hatching eggs per egg sac) was 81.4 ± 30.9% (*n* = 57; range = 1–100%) (Tables 3, 4). The number of eggs (t = 1.6; $P > 0.05$; df = 54), spiderlings (t = 1.1; $P > 0.05$; df = 54) and non-viable eggs (t = 0.53; $P > 0.05$; df = 54) did not significantly differ between the first

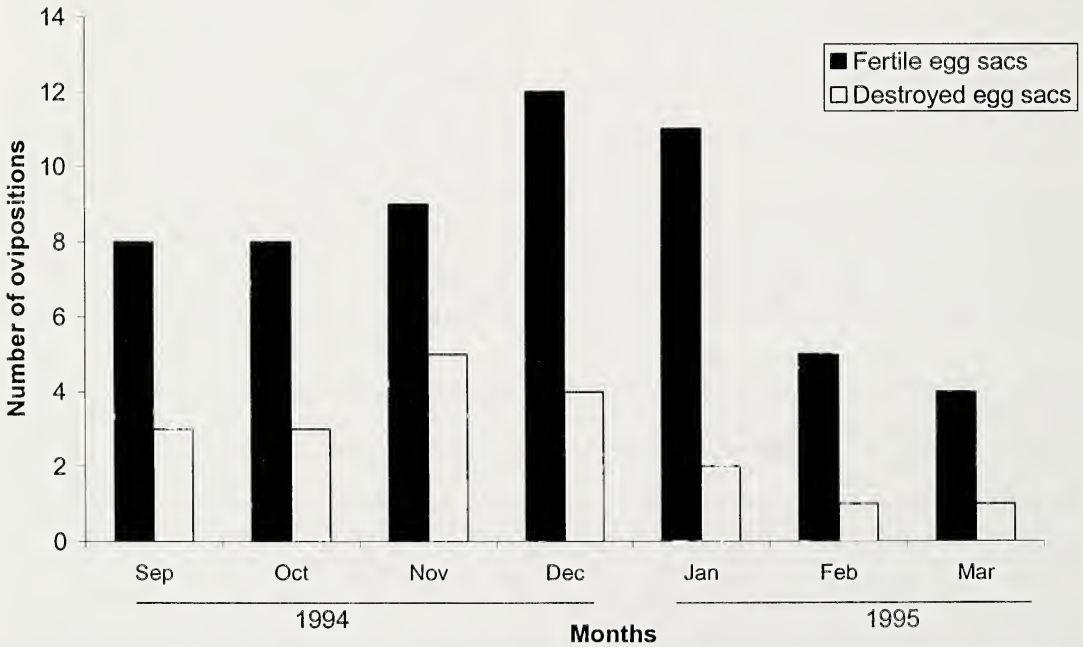


Figure 2.—Ovipositions by 36 *Loxosceles intermedia* females of unknown reproductive histories in the laboratory, from September 1994–March 1995.

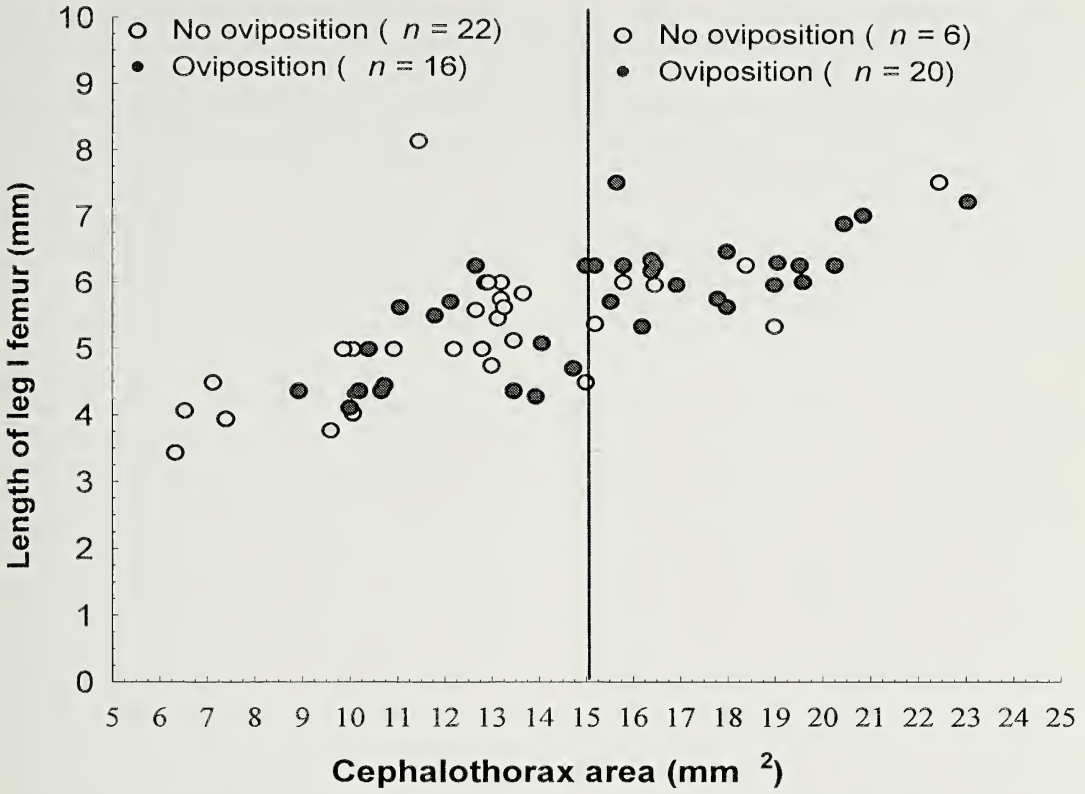


Figure 3.—Relationship between the sizes of female *Loxosceles intermedia*, leg I femur length and cephalothorax area with an unknown reproductive history and the tendency to lay eggs.

Table 3.—Fecundity in the laboratory for *Loxosceles intermedia* with an unknown reproductive history (the values are the mean ± SD with the sample size (*n*) and range in parentheses).

	1st oviposition		2nd oviposition		3rd oviposition		Total	
	n	Average	*n*	Average	*n*	Average	*n*	Average
	48		2		1		76	
# of egg sacs			7					
# of fertile egg sacs	36		2		1		57	
			0					
# of destroyed egg sacs	12		7		—		19	
Total number of eggs	19	53 ± 23.3	6	43.1 ± 19	—	47 (*n* = 1)	2823	49.4 ± 21.9
	08	(36; 6–92)	2	(20; 8–84)				(57; 6–92)
Spiderlings	15	44.2 ± 17	3	36.5 ± 21	—	30 (*n* = 1)	2351	41.2 ± 25
	91	(36; 2–92)	0	(20; 7–84)				(57; 2–92)
Egg viability (%)	—	80.3 ± 31	—	85.7 ± 25	—	64 (*n* = 1)	—	81.8 ± 28
		(36; 2–100)		(20; 15–100)				(57; 2–100)
Undeveloped eggs	31	8.2 ± 15.9	3	6.6 ± 11.8	—	36 (*n* = 1)	466	8.5 ± 14.9
	7	(36; 0–80)	2	(20; 0–41)				(57; 0–80)
Incubation time (days)	—	46.2 ± 9.5	—	47.9 ± 14.1	—	65 (*n* = 1)	—	47.1 ± 11.4
		(32–45)		(20; 37–92)				(57; 32–92)

Table 4.—Variables for fertile egg sacs from *L. intermedia* with unknown reproductive histories maintained in the laboratory (September 1994–March 1995). (The values are the mean ± SD with the sample size (*n*) and range in parentheses.)

	n	Mean ± SD	Range
Female cephalothorax area (mm^2)	57	15.5 ± 3.7	8.9–23.1
Female weight (mg)	57	103.9 ± 53.4	34.6–264
Spiderling weight (mg)	57	0.078 ± 0.048	0.001–0.0024
Temperature during the incubation period (°C)	57	23.8 ± 2.1	20.9–29.2
Air humidity during the incubation period (%)	57	72.6 ± 5.5	63.3–88.7
Latency between ovipositions (days)	20	68.8 ± 25.8	18–136

and second ovipositions (Tables 3, 4), despite a tendency to increase.

The length of incubation appeared to be related to air temperature and relative humidity. Most of the fertile ovipositions were incubated at 21 °C to 27 °C at a relative air humidity of 64–76%. Larger females tended to deposit more eggs ($r^2 = 0.062$; $P = 0.06$; $n = 57$; df = 56), with a slight but significant correlation between female weight *vs* the number of eggs ($r^2 = 0.072$; $P < 0.05$; $n = 57$; df = 56).

There was no correlation between spiderling weight or latency to oviposition and the total number of eggs, spiderlings or non-viable eggs. ($r^2 = 0.008$, $P = 0.4$, df = 105; $r^2 = -0.0003$, $P = 0.3$, df = 105; $r^2 = -0.018$, $P = 0.9$, df = 105 and $r^2 = 0.003$; $P = 0.2$, df = 105; $r^2 = 0.003$; $P = 0.2$; df = 105; $r^2 = 0.009$; $P = 0.9$; df = 105, respectively).

In the case of destroyed egg sacs, the average time in which they remained intact was 8 ± 8.3 days ($n = 19$; range = 0–26 days). Five eggs which fell from destroyed egg sacs, developed normally. Their temperature and relative humidity during the incubation period are shown in Table 5.

Females remained close to the egg sac throughout the whole incubation period. Four females opened the egg sac about six days before the eggs hatched. In one of these cases, the female spider ate the spiderling.

The average weight of the wild-caught females (105.3 ± 57 mg [$n = 36$; range = 39.7–264.8]) did not differ of the spiders reared at laboratory (107.8 ± 5.1 mg [$n = 75$; range = 101–118]) ($t = -0.3$; $P = 0.7$; df = 108). In egg sacs from females with unknown reproductive histories, the average number of spiderlings (41.2) (U = 2151; $P < 0.01$), the total number of eggs (49.5) (U = 2788.5; $P < 0.01$) per egg sac, and the average percentage of egg viability (82.7%) (U = 2120.5; $P < 0.001$) were greater than in females subjected to only one mating (29.4, 36.5 and 70.2%, respectively). Nevertheless, the average number of unhatched eggs per egg sac (U = 2323.5; $P < 0.01$) and the duration of incubation (U = 2033; $P < 0.001$) were greater in females with one mating than in those with unknown reproductive histories.

DISCUSSION

The egg sac construction of *L. intermedia* (behavior and time), and oviposition of the egg in the number of sacs agree with the reported patterns for the genus (Galiano 1967 for *L. laeta*; Hite et al. 1966 and Horner & Stewart 1967 for *L. reclusa* and Rinaldi et al. 1997 for *L. gaucho*). Only Delgado's (1966) description for *L. rufipes* was different. This author noted that oviposition required one to

Table 5.—Variables related to egg sacs destroyed by *L. intermedia* with unknown reproductive histories in the period from September 1994–March 1995. (The values are the mean ± SD with the sample size (*n*) and range in parentheses.)

	n	Mean ± SD	Range
Incubation period (days)	19	8.42 ± 8.3	0–26
Temperature during the incubation period (°C)	19	22.3 ± 2.3	18–25.3
Air humidity during the incubation period (%)	19	69.6 ± 1	51.9–87

two weeks and that the female positioned herself over the egg sac within a silk covering.

Females with unknown reproductive histories produced up to three fertile consecutive egg sacs and the period of egg-laying was restricted to seven out of the 18 months observed. On the other hand, females with only one insemination constructed up to four fertile egg sacs during 26 of 48 months of observation. Hite et al. (1966) reported similar results for *L. reclusa*, in which already mated females produced a smaller number of egg sacs than females mated only once in the laboratory. However, the possibility that the females deposited other egg sacs could account for the results of the latter study, the difference between our results and those of Andrade et al. (2000). In these studies already fertilized *L. intermedia* oviposited up to five times. Despite the probable relationships between spider weight and size and the number of eggs produced, the number of egg sacs is very similar among many species of the genus. For *L. hirsuta*, up to the three fertile egg sacs have been reported (Fischer & Marques da Silva 2001). For *L. gaucho*, 56.5% of the females that constructed more than one egg sac oviposited three or four times (Rinaldi et al. 1997) and Bücherl (1961) also reported that *L. laeta* and *L. gaucho* laid up to three egg sacs. For *L. reclusa* (Hite et al. 1966) and *L. laeta* (Galiano & Hall 1973), 5–15 ovipositions per female have been observed. However, these data were not confirmed by later studies of *L. reclusa* (up to three egg sacs) (Horner & Stewart 1967) and *L. laeta* (up to four egg sacs) (Andrade et al. 2000).

The total number of eggs and number of fertile eggs was significantly greater in females with unknown reproductive histories, suggesting that these spiders may have been fertilized more than once or were healthier from living in the wild. It is possible that multiple matings can favor reproductive success resulting in a larger number of fertile eggs than females that copulated once. The same point can be made about multiple egg sacs. According to Horner & Stewart (1967), female *L. reclusa* that mated repeatedly during the season were more fertile since additional mating protected against the gradual loss of sperm viability and inadequate storage capabilities.

Oviposition was more frequent in larger females which also tended to lay a greater total number of eggs and more eggs per egg sac. These observations indicate the importance of foraging success on fertility. Interspecific variations have been recorded for *L. laeta* and *L. intermedia* (Andrade et al. 2000) with the former species laying a greater number of eggs because of its greater size and weight. The average number of eggs per egg sac varies considerably in *Loxosceles*, e.g. 50.1 in *L. reclusa* (Hite et al. 1966), 61.3 in *L. gaucho* (Rinaldi et al. 1997), 33.7 in *L. hirsuta* (Fischer & Marques da Silva 2001), and 88.4 in *L. laeta* (Galiano 1967). Various factors, including the female's physiological state, can influence those results since an average of only 23 eggs per egg sac has been reported for *L. reclusa* (Horner & Stewart 1967). Rinaldi et al. (1997) attributed the low values reported by Bücherl (1961) for *L. laeta* and *L. gaucho* (12–15 eggs per egg sac) to the construction of egg sacs during female senescence. The existence of morphological and numerical variations in the seminal receptacles of *L. intermedia* females must also be considered (Buckup 1980; Fischer 1994), with the relationships between the number of receptacles, their functionality and female fecundity requiring further detailed studies. For the females reared in the laboratory, the number of viable eggs of *L. intermedia* correlated with the duration of mating and female age. According to Rinaldi et al. (1997), if the first mating in *L. gaucho* females lasted more than double the female's age, number of offspring per oviposition was lower. In the Lyniphiidae, the relationship between the duration of mating and egg viability was related to the time required for the transfer of sufficient sperm for the construction of three egg sacs (Suter & Parkhill 1990).

The length of incubation in *L. intermedia* appeared to be related to the air temperature and relative humidity, and these factors appeared to influence how long the spiderlings remained within the egg sac. Similar studies have reported values of 36.7 days for *L. reclusa* (Hite et al. 1966), 40.1 days for *L. gaucho* (Rinaldi et al. 1997) and 56.9 days for *L. hirsuta* (Fischer & Marques da Silva 2001), and these appear to be little affected by variations in the environmental conditions. The time interval between consecutive oviposition may also be influenced by the spiders'

nutritional state, sperm storage and stress since there was an increase in this interval after the second oviposition. In the present study, females with unknown reproductive histories had smaller intervals (68.8 days) than females with one mating (116.7 days), although a greater number of egg sacs were observed in the former

Loxosceles intermedia thus has a greater interval between oviposition than *L. gaucho* (39.2 days) (Rinaldi et al. 1997) and *L. reclusa* (32 days) (Horner & Stewart 1967).

The average number of non-viable eggs did not differ between the two groups, although non-viable eggs were seen in 63.2% of the egg sacs produced by female *L. intermedia* with unknown reproductive histories compared to 83.5% in females with only one mating. The presence of non-viable eggs could reflect a lack of fertilization, the interruption of development because of environmental or biological conditions and the possibility that these eggs were eaten by older spiderlings. Non-viable eggs have also been reported for *L. hirsuta* (42.7% of cases: Fischer & Marques da Silva 2001) and for other spider groups (Valério 1974; Anderson 1978; Christenson et al. 1979; Downes 1985; Gonzales 1989).

The decrease in the number of viable eggs in successive egg sacs was insignificant in females fertilized only once. Contrary to the findings of Eberhard (1979), a reduction in the number of eggs in successive ovipositions has also been observed in *L. hirsuta* (Fischer & Marques da Silva 2001), *L. gaucho* (Rinaldi et al. 1997) and other spiders (Downes 1985; Gonzales 1989; Willey & Adler 1989; Suter 1990; Wheeler et al. 1990).

The destruction of egg sacs may have been influenced by various factors. In females which did not oviposit more and which later destroyed their egg sac, this behavior may have been influenced by physiological conditions such as infertility, age, nutrient shortage or stress. Also, since sperm storage was not an important factor in egg sac destruction, the influence of air temperature, relative humidity and stress must be considered. Although the relationship between the incubation length and the air temperature and relative humidity was low, there nevertheless appeared to be some minimum requirements for oviposition and egg development to occur. The destruction of egg sacs by females has been recorded for *L. reclusa* (Hite et al. 1966) in which the females sometimes ate their own eggs and the eggs in some egg sacs did not eclode. In *L. hirsuta*, 55.6% of the females that destroyed their egg sacs constructed other fertile sacs. A similar behavior was observed in *Lycosa malitiosa* Tullgren 1905 (Lycosidae) (Capocasale et al. 1984) and was attributed to the peak of synchronization between the spontaneous opening of the egg sac by the mother and spiderling development. As observed here, Horner & Stewart (1967) also noted that *L. reclusa* spiderlings did not need help to leave the egg sac, but if the mother was present, she helped to tear the egg sac.

Reproductive success in *L. intermedia* is influenced by numerous factors that can affect spider fertility, including: air temperature, relative humidity, length of mating, female weight, and female age. These factors are relevant for *L. intermedia* since these spiders live in and around buildings and are, therefore subject to smaller oscillations of environmental conditions, have food in abundance, have large populations with numerous males that can potentially inseminate any given females, the fecundity is likely to be high and could explain the abundance of this species in Curitiba.

ACKNOWLEDGMENTS

The authors thank Prof. Dr. Luís Amilton Foerster, Dra. Sylvia Lucas and Dra. Gail Stratton for their comments and help in preparing this manuscript and Liliani Tiepolo and Claudia Staudacher for supplying the female *L. intermedia*. This paper is suported by Curso de Pós-Graduação em Zoologia—Universidade Federal do Paraná—UFPR and CAPES. J. Vasconcellos-Neto was supported by a grant from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, grant no. 300539/94-0) and BIOTA/FAPESP—The Biodiversity Virtual Institute Program (grant no. 99/05446-8).

LITERATURE CITED

Anderson, J.F. 1978. Energy content of spiders eggs. Oecologia 37:41–57.

Andrade, R.M.G., W.R. Lourenço & D.V. Tambourgi. 2000. Comparison of the fertility between *Loxosceles intermedia* and *Loxosceles laeta* spiders (Araneae, Sicariidae). Journal of Arachnology 28:245–247.

Begon, M.J., L. Harper, & C.R. Towsend. 1990.

Ecology of Individuals, Populations and Communities. Cambridge: Blackwell Scientific Publications.

Bücherl, W. 1961. Aranhas do gênero *Loxosceles* e loxoscelismo na América. Ciência e Cultura 13: 213–224.

Buckup, E.H. 1980. Variação interpopulacional dos receptáculos seminais em aranhas do grupo Spadicea do gênero *Loxosceles* Heinecken & Lowe, 1832 (Araneae; Scytodidae). Hieringia série Zoologia 55:137–147.

Capocasale, R.M., F.G. Costa & J.C. Moreno. 1984. La produción de ootecas de *Lycosa malitiosa*, Tullgren (Araneae, Lycosidae). II Analisis cuantitativo de hembras virgenes e copuladas. Aracnologia 3:1–7.

Christenson, T.E., P.A. Wenzl & P. Legum. 1979. Seasonal variation in egg hatching and certain egg parameters of the golden silk spider *Nephila clavipes* (Araneae). Psyche 2:137–147.

Christenson, T.E. & P.A. Wenzl. 1980. Egg laying of the golden silk spider, *Nephila clavipes* L. (Araneae, Araneidae): functional analysis of the egg sac. Animal Behaviour 28:1110–1118.

Cooke, J.A.L. 1965. A contribution to the biology of the British spiders belonging to the genus *Dysdera*. Oikos 6:20–25.

Costa, F.G. & R.M. Capocasale. 1984. La producción de ootecas de *Lycosa malitiosa* Tullgren (Araneae:Lycosidae). Importancia de la muda de maturacion sobre la primera oviposición. Aracnologia 2:1–8.

Delgado, A. 1966. Investigación ecológica sobre *Loxosceles rufipes* (Lucas), 1834 en la región costera del Perú. Memórias do Instituto Butantan 33:683–688.

Downes, M.F. 1984. Egg sac "theft" among *Latrodectus hasselti* females (Araneae, Theridiidae). Journal of Arachnology 12:244.

Downes, M.F. 1985. Fecundity and fertility in *Latrodectus hasselti*. Australian Journal of Ecology 10:261–264.

Downes, M.F. 1987. Postembryonic development of *Latrodectus hasselti* Thorell (Araneae, Theridiidae). Journal of Arachnology 14:293–301.

Downes, M.F. 1988. The effect of temperature on oviposition interval and early development in *Theridion rufipes* Lucas (Araneae, Theridiidae). Journal of Arachnology 16:41–45.

Eberhard, W.G. 1979. Rates of egg production by tropical spiders in the field. Biotropica 11:292–300.

Enders, F. 1976. Clutch size related to hunting manner of spider species. Annals of the Entomological Society of America 69:991–998.

Figueira, J.E.C. & J. Vasconcellos-Neto. 1993. Reproductive success of *Latrodectus geometricus* (Theridiidae) on *Paepalanthus bromelioides* (Eriocaulaceae): rosette size, microclimate, and prey capture. Ecotropicos 5:1–10.

Fink, L.S. 1986. Costs and benefits of maternal behaviour in the green lynx spider (Oxyopidae, *Peucetia viridans*). Animal Behaviour 34:1051–1060.

Fischer, M.L. 1994. Levantamento das espécies do gênero *Loxosceles* Heinecken & Lowe, 1832 no município de Curitiba, Paraná, Brasil. Estudos de Biologia 38:65–86.

Fischer, M.L. & E. Marques da Silva. 2001. Oviposição e desenvolvimento de *Loxosceles hirsuta* Mello-Leitão, 1931 (Araneae; Sicariidae). Estudos de Biologia 47:15–20.

Fischer, M.L. & J. Vasconcelos-Neto. 2000. Comportamento sexual de *Loxosceles intermedia* Mello-Leitão, 1934 (Araneae; Sicariidae). Revista de Etologia 2:31–42.

Foelix, R.F. 1996. Biology of Spiders. New York. Oxford University Press.

Fritz, R.S. & D.H. Morse. 1985. Reproductive success and foraging of the crab spider *Misumena vatia*. Oecologia 65:194–200.

Galiano, M.E. 1967. Ciclo biologico e desarollo de *Loxosceles laeta* (Nicolet,1849). Acta Zoologica Lilloana 23:431–464.

Galiano, M.E. & M. Hall. 1973. Datos adicionales sobre el ciclo vital de *Loxosceles laeta* (Nicolet) (Araneae). Physis 32:277–288.

Gonzalez, A. 1989. Analisis del comportamiento sexual y producción de ootecas de *Theridion rufipes*. Journal of Arachnology 17:129–136.

Hite, M.J., W.J. Gladney., J.L LancasterJR, & W.H. Whitcomb. 1966. Biology of brown recluse spider. Arkansas Agriculture Experimental Station Bulletin 711:2–26.

Hoffmaster, D.K. 1982. Predator avoidance behaviors of five species of Panama orb-weaving spiders (Araneae; Araneidae, Uloboridae). Journal of Arachnology 10:69–73.

Horner, N.V. & K.W. Stewart. 1967. Life history of the brown spider, *Loxosceles reclusa* Gertsch and Mulaik. Texas Journal of Sciences 19:333–347.

Jackson, R.R. 1978. Life history of *Phidippus johnsoni* (Araneae, Salticidae). Journal of Arachnology 6:1–29.

Killebrew, D.W. & N.B. Ford. 1985. Reproductive tactics and female body size in the green lynx spider *Peucetia viridans* (Araneae, Oxyopidae). Journal of Arachnology 13:375–382.

Krafft, B. 1982. The significance and complexity of communication in spiders. Pp. 15–66. *In* Spider Communication: Mechanisms and Ecological Significance (P.N. Witt & J. S. Rovner, eds.). Princeton University Press, Princeton, New Jersey.

Levy, G. 1970. The life cycle of *Thomisus onustus* (Thomisidae: Araneae) and outlines for the clas-

sification of the life histories of spiders. Zoology 160:523–536.

Miyashita, K. 1987. Development and egg sac production of *Achaearanea tepidariorum* (C.L. Koch) (Araneae; Theridiidae) under long and short photoperiods. Journal of Arachnology 15: 51–58.

Muniappan, R. & H.L. Chada. 1970. Biology of the crab spider, *Misumenops celer*. Annals of the Entomological Society of America 63:1718–1722.

Nuessly, G.R. & R.D. Goeden. 1984. Aspects of the biology and ecology of *Diguetia mojavea* Gertsch (Araneae, Diguetidae). Journal of Arachnology 12:75–85.

Opell, B.D. 1984. A simple method for measuring desiccation resistance of spider egg sacs. Journal of Arachnology 12:245.

Rinaldi, I.M.P., L.C. Forti, & A.A. Stropa. 1997. On the development of the brown spider *Loxosceles gaucho* Gertsch (Araneae; Sicariidae): the nympho-imaginal period. Revista Brasileira de Zoologia 14:697–706.

Ruttan, L.M. 1991. Effects of maternal presence on the growth and survival of subsocial spiderlings (Araneae: Theridiidae). Insect Behaviour 4:251–257.

Suter, R.B. 1990. Courtship and the assessment of virginity by male bowl and doily spiders. Animal Behaviour 39:307–313.

Suter, R.B. & V.S. Parkhill. 1990. Fitness consequences of prolonged copulation in the bowl and doily spider. Behaviour, Ecology, and Sociobiology 26:369–373.

Turnbull, A.L. 1962. Quantitative studies of the food of *Linyphia triangularis* Clerk (Araneae; Linyphiidae). Canadian Entomology 91:1233–1237.

Wheeler, G.S., J.P. McCaffrey, & J.B. Johnson. 1990. Developmental biology of *Dictyna* spp (Araneae: Dictynidae) in the laboratory and field. American Midland Naturalist 123:124–134.

Willey, M.B. & P.H. Adler. 1989. Biology of *Peucetia viridans* (Araneae, Oxyopidae) in South Carolina, with special reference to predation and maternal care. Journal of Arachnology 7:275–284.

Manuscript received 9 June 2003, revised 15 June 2004.

2005. The Journal of Arachnology 33:681–702

REFINING SAMPLING PROTOCOLS FOR INVENTORYING INVERTEBRATE BIODIVERSITY: INFLUENCE OF DRIFT-FENCE LENGTH AND PITFALL TRAP DIAMETER ON SPIDERS

Karl E.C. Brennan, Jonathan D. Majer and **Melinda L. Moir**: Department of Environmental Biology, Curtin University of Technology, GPO Box U1987, Perth WA 6845, Australia. E-mail: kbrennan@unimelb.edu.au

ABSTRACT. The limited resources available to inventory biodiversity and conduct ecological monitoring requires efficient protocols for sampling with pitfall traps. Here we consider adding different length drift-fences to pitfall traps on spiders. Four different fencing treatments (no fence, or fence lengths of 2, 4 and 6 m) were evaluated in combination with three trap diameters (4.3, 7.0 and 11.1 cm). Three-way ANOVAs revealed no significant interaction effects between any combinations of fencing treatments, trap size or the spatial positioning of transects within the study site along which traps were arranged. Post-hoc tests showed fences significantly increased the abundance of individuals and richness of spider families, and species collected. Traps with 6 m fences were significantly higher in all of these variables than traps with 2 m fences. ANOSIMs revealed taxonomic composition differed significantly between fenced and unfenced traps at familial, and specific ranks. Among fenced traps, taxonomic composition was influenced primarily by trap diameter rather than fence length. ANOSIMs showed significant differences in taxonomic composition between each trap diameter for fenced traps. An optimal combination of fencing treatment and trap diameter was determined by constructing smoothed species accumulation curves for increasing numbers of traps. Four criteria were considered: equivalent numbers of traps, standardized cumulative trap circumference, standardized cumulative fence length (fenced traps only) and standardized cumulative handling time. For the same number of traps, 11.1 cm traps with 4 and 6 m fences collected the most species. At a standardized trap circumference, long fences were best, with all trap sizes catching similar numbers of species. When fence length was standardized, 11.1 cm traps with 2 or 4 m fences collected the most species. At a standardized handling time all traps caught very similar numbers of species, although most 11.1 cm diameter traps collected more species than other trap sizes and those with 4 m fences were most efficient. Given the similar performance of fenced and unfenced traps for standardized handling time, we outline reasons why unfenced traps may be best.

Keywords: Arthropods, barriers, guides, inventory, sampling methods

Little doubt exists that global biodiversity is decreasing rapidly (Chappin et al. 2000; Pimm & Raven 2000; Purvis & Hector 2000). Calls have been made to inventory global species diversity (Wilson 1985; Raven & Wilson 1992; Stork & Samways 1995), however, there are inadequate resources available for this task (May 1988; Gaston & May 1992; Hawksworth 1995). Methods that sample taxa quickly and efficiently are needed (Colwell & Coddington 1995; Dobyns 1997). Additionally, limitations of sampling methods, or deviations from an accurate representation of community structure, must be known (Churchill 1993; Churchill & Arthur 1999; Skerl & Gillespie 1999). Rapid development and acceptance of standardized sampling protocols represents a key conservation goal as it facilitates comparisons between studies where to date, comparisons have been either tenuous or impossible (Coddington et al. 1991; Beattie et al. 1993; New 1999). Standardized sampling protocols have recently been advanced for ground dwelling ants and beetles (Agosti & Alonso 2000; Niemelä et al. 2000). Standardized methods will facilitate comparisons between studies and renew interest in their use for ecological monitoring.

Considerable refinements for collecting spiders have been made. Horizontal stratification by different spider families and species within habitats has long been known (Muma &

Muma 1949; Turnbull 1973, Merrett 1983). To target all habitat strata many different collecting techniques are required. Moreover, given the heterogeneous nature of spider communities, sampling needs to be conducted over different spatial and temporal scales (Churchill & Arthur 1999). Comparisons of methods to date include pitfall trapping, beating, sweep-netting, suction sampling with D-vac or other devices, extraction from litter by Tullgren funnels or hand, and hand collecting from different non-canopy habitat strata (Duffey 1962; Uetz & Unzicker 1976; Merrett & Snazell 1983; Coddington et al. 1991, 1996; Topping & Sunderland 1992; Edwards 1993; Churchill 1993; Samu & Sárospataki 1995; Dobyns 1997; Churchill & Arthur 1999; Standen 2000). The standardized sampling protocol advanced by Coddington et al. (1991, 1996) targeted spiders in all non-canopy habitat strata. Their collecting methods were beating, hand collecting looking-up, hand-collecting looking-down, and extraction of spiders from leaf litter with Tullgren funnels or by hand. They suggested that using pitfall traps in combination with the above methods might be beneficial. Considerable sampling biases and limits to data interpretation are known for pitfall traps (Greenslade 1964; Southwood 1966; Adis 1979; Spence & Niemelä 1994; Melbourne 1999). Despite this, many authors have found pitfall traps valuable in their collecting repertoire (Duffey 1972; Uetz & Unzicker 1976; Churchill 1993). Establishing a standardized pitfall trapping protocol for inventorying spiders is needed (Brennan et al. 1999).

Many advances in sampling with pitfall traps have been made. Various materials and designs have been used to construct invertebrate pitfall traps, including cups, cans, jars and troughs (Duffey 1962; Merrett 1967; Luff 1975). Refinements increasing capture success of spiders have included fitting aprons around pitfall traps; this increased the catch of clubionids, gnaphosids, salticids and thomisids (Cutler et al. 1975; Uetz & Unzicker 1976). Aprons may also reduce sampling error arising from alteration of microclimate, disturbance by mammals, flooding, and litter fall (Uetz & Unzicker 1976). Traps containing a killing/preserving solution collect more spiders than dry traps (Curtis 1980; Gurdebeke & Maelfait 2002), and adding detergent to ethylene glycol catches more linyphiids (Topping & Luff 1995). Funnels placed inside traps decrease captures, but by decreasing evaporation of ethanol can yield better specimens for DNA analysis (Gurdebeke & Maelfait 2002). With roughened surfaces on the interior of pitfall traps (including wear from reuse) collection of linyphiids declines (Topping & Luff 1995). Larger diameter traps collect more species than smaller traps (Brennan et al. 1999; Work et al. 2002). Large traps are more efficient than smaller traps when measured by handling time (Brennan et al. 1999). Size of rain covers has no effect on spider catch (Work et al. 2002). Length of trapping period can influence interpretation of community composition for linyphiids and other surface-active spiders, with longer periods of collecting preferable (Topping & Luff 1995; Riecken 1999). More traps collect more species (Samu & Lövei 1995), although taxonomic composition remains fairly constant with fewer traps (Niemelä et al. 1986; Riecken 1999). Consequently, where resources are limited, decreasing the number of traps, rather than sampling period, may permit more accurate interpretation of community structure (Riecken 1999).

Recently, attaching fences to pitfall traps to facilitate spider captures has aroused interest. Different authors have used the terms "barriers", "drift-fences", "fences" and "guides" synonymously and for different structures. Here "fences" refers to structures erected to guide surface-active animals into traps. These differ from structures erected to form an enclosure around traps, which limits the spatial area from which traps sample (e.g. Gist & Crossley 1973; Mommertz et al. 1996; Holland & Smith 1999). In savanna woodland and mown lawn of tropical northern Australia fences increase the catch of spiders and many dominant spider taxa. The effectiveness of fences, however, varies over time (Churchill unpub. data). The taxonomic composition of spiders collected also varies with trap design. Trap size differences (4.5 cf. 8 cm diameter traps) were greatest between unfenced compared to fenced traps (Churchill unpub. data).

Here we determine: 1) if fences increase spider catchability in the jarrah (*Eucalyptus marginata*) forest of temperate south-western Australia, and 2) if fence length influences taxonomic richness and composition? 3) For

fenced traps, does trap size influence taxonomic richness and composition? 4) How many traps are required, and what is the optimum combination (trap diameter and fence length) for sampling spiders in this habitat? Our optimal combination is based on catching the most species using the: a) least number of traps; b) lowest sampling intensity (minimal cumulative trap circumference); c) least amount of fence; and d) least amount of time.

METHODS

Study site.—Spiders were collected from unmined forest surrounding Alcoa World Alumina Australia's (formerly Alcoa of Australia) Jarrahdale mine (32°17′ S, 116°08′ E) on the Darling Plateau, approximately 45 km southeast of Perth. The region has a Mediterranean climate, with hot dry summers and cool wet winters. Annual rainfall is 1200 mm, with most falling between May and September. Soils are highly weathered and composed of coarse ferrinous gravel (> 2 mm particle size) in a matrix of yellow-brown sand derived from a lateritic profile (Churchward & Dimmock 1989).

Vegetation at the site (450 × 250 m) was a tall forest (to 35 m) of jarrah and marri (*Corymbia calophylla*) trees. Other small trees (3–7 m) were present also; mainly Bull Banksia (*Banksia grandis*), and Snottygobble (*Persoonia longifolia*). These overtopped understorey species such as grass-trees (*Xanthorrhoea preissii* and *Kingia australis*), cycads (*Macrozamia riedlei*) and legumes (*Acacia*, *Bossiaea* and *Kennedia*). Leaf litter varied from 25–100 % cover and a depth of 1–40 mm.

Sampling spiders.—Effects of pitfall trap size and fence length on spider catchability were investigated using a three-way factorial design, composed of pitfall trap diameters (4.3, 7.0 and 11.1 cm), fence length (0, 2, 4 and 6 m) and spatial positioning of transects within the study site along which the pitfall traps were arranged. Pitfall traps were arranged as follows: 15 parallel transects were positioned 30 m apart. Along each transect 12 traps were positioned 14 m apart with each trap representing a different combination of trap size and fencing treatment (3 trap diameters × 4 fence lengths = 12 traps per transect, 12 traps × 15 transects = 180 traps). Transects were grouped into three sets based on their location within the site; southern (transects 1–5), central (transects 6–10) and northern (transects 11–15). This design permitted potential differences in spider catchability related to the spatial positioning of transect groups within the study site to be considered. For brevity, focus is restricted here to trap diameter and fence length.

Pitfall traps were clear plastic containers that varied in diameter but not depth (7.5 cm). Each trap comprised three plastic containers. The first was dug into the soil so that its rim was flush with the soil surface. The second was filled with soil, placed inside the first container, and left *in situ* for two weeks. This was to allow any disturbance effects caused by "digging in" the traps to abate (Joosse & Kapteijn 1968; Greenslade 1973). For trapping, the soil-filled container was removed and replaced with a third that was half-filled with Galts solution (Main 1976) plus 2 ml of detergent (to decrease surface tension). The use of this solution is no longer recommended. To ensure that the rim of the third trap was flush with the soil surface a small amount of soil was added where necessary. Traps were open for one week (12–19 September 1997).

Fences consisted of black plastic (200 um thick), approximately 25 cm high and buried 5 cm into the ground. They were aligned parallel to transects and secured with wooden skewers (0.25 cm diameter, 20 cm long) where necessary. Fences did not span the trap but were cut into two pieces and orientated such that an imaginary line joining the two fences together would bisect the pitfall trap into equal halves. Considerable care was taken to ensure that fence edges closest to each trap were not folded against the outer rim (which might have prevented a spider moving along the fence to fall into the trap). Traps were checked on the third day of sampling. Any litter debris that had fallen into the trap and was likely to reduce retaining efficiency was removed.

Adult spiders were sexed and identified to species level and assigned a code when no name could be found. Most species at Jarrahdale are undescribed and many older taxonomic keys are inadequate (Brennan et al. 2004). Juveniles, penultimate instar males and sub-adult females could not be identified with certainty beyond family level (and sometimes genus), so are not considered here. A refer-

ence collection of taxa has been deposited in the Western Australian Museum.

Data analysis.—Data were analyzed using univariate and multivariate analyses plus species accumulation curves (collectors curves).

Univariate analysis: Univariate analyses involved three-way and two-way analysis of variances (ANOVAs) that had Type III sums of squares (Underwood 1997). Dependent variables were abundance, and taxon richness at familial and specific rank. Factors were FENCE, TRAP and LOCATION. Levels for FENCE were the fence lengths 0, 2, 4 and 6 m. Levels for TRAP were the trap sizes 4.3, 7.0 and 11.1 cm. Levels for LOCATION were southern, central and northern.

Our full data set included all combinations of fence length and trap size across all transects. It was analyzed using three-way ANOVAs. Means for each trap size were derived from all traps comprising that size class (n = 60) and means for each fence length were derived from all traps comprising that fence length (n = 45); means for each location were derived from all traps from the five transects making up each location (n = 60).

For fenced traps, the effect of trap size on species richness was considered separately for each fence length. Three data subsets were analyzed with two-way ANOVAs: short fences (traps with 2 m fences); medium fences (traps with 4 m fences); and long fences (traps with 6 m fences). For each subset, factors considered were TRAP and LOCATION, with species richness being the dependent variable. Means for each trap size were derived from all traps within the fence length being considered (n = 15). Means for each location were derived from all traps within the fence length being considered (n = 15).

The effect of fence length on species richness was also considered separately for each trap size. Three data subsets, namely those from small traps (4.3 cm diameter), medium traps (7.0 cm diameter), and large traps (11.1 cm diameter) were analyzed using two-way ANOVAs. For each subset, factors considered were FENCE and LOCATION with species richness being the dependent variable. Means for each fence length were derived from all traps within the trap diameter being considered (n = 15). Means for each location were derived from all traps within the trap diameter being considered (n = 15).

Assumptions of ANOVA were considered before analysis. Abundance data were transformed to the log of the value plus one, while family and species richness were transformed to the square root of the value plus 0.5 (Zar 1984). Post-hoc means comparisons utilized Scheffé's S test (Day & Quinn 1989). Variance ratios (F) were considered significant when $P < 0.05$. All univariate analysis were performed using SPSS 7.5 (SPSS 1996).

Multivariate analysis: To determine the influence of different trap diameter/fence length combinations on the taxonomic composition of spiders, we used the Bray-Curtis (1957) measure to construct a similarity matrix on standardized root transformed data. The Bray-Curtis measure takes the form, $C = 2w/(x + y)$, where x is the number of adults collected by one method, y is the total number of adults collected by another method, and w is the sum of the lesser values for those species present in both samples. Standardization limits differences between samples that may arise through differences in abundance by dividing each count by the total abundance of all species within each collecting method. Root transformation reduces the influence of the most abundant species to dominate results (Clarke & Green 1988).

For ease of interpreting similarities, nonmetric multidimensional scaling (1,000 iterations) was used to represent data in two-dimensional ordination space (Clarke 1993). Confirmation of interpretations from MDS was obtained by hierarchical clustering, with group-average linking. Analysis of similarities (ANOSIMs, see Clarke & Green 1988) were used to test for differences in taxonomic composition between: a) unfenced and fenced traps (unfenced vs. fences of lengths 2, 4, and 6 m); b) trap sizes (4.3 vs. 7.0 vs. 11.1 cm diameter) irrespective of fencing; c) fencing treatments (unfenced vs. 2 m vs. 4 m vs. 6 m fences); d) fenced traps with different diameters (4.3 vs. 7.0 vs. 11.1 cm). An understanding, of which species made the greatest contribution to our MDS and ANOSIM results, was obtained through similarity percentages (SIMPER, see Clarke 1993) on root-transformed standardized data with cut-off contributions set at 50 %.

To determine whether results held at a higher taxonomic rank, we also constructed a similarity matrix on standardized, root trans-

formed family level data. A Mantel's test (1,000 randomizations) using Spearman's Rank correlation (Manly 1994) was then used to test for a relationship between the species and family level matrices. Finally the MDS, hierarchical clustering, and ANOSIMs outlined above were repeated at familial rank. For brevity only the MDS results are presented. All multivariate analyses were performed using Primer 5.2.2 (Primer-E 2001).

Species accumulation curves: To determine an optimal combination of trap size/fence length we standardized at equivalent measures of collecting effort on randomized species accumulation curves (Colwell & Coddington 1995). Curves plotted cumulative species richness versus increasing numbers of traps, smoothed through 10,000 iterations. This method allowed integration of patchiness in species occurrences between samples that is lost when samples are pooled with classical rarefaction (Colwell 1994–2000). Curves were produced using EstimateS 5.0 (Colwell 1994–2000).

An optimal combination of trap size/fence length was determined for four measures of collecting effort, namely; number of traps, trap circumference, fence length and handling time. The optimal trap size/fence length combination for a standardized number of traps was that which gave the greatest species richness for 15 traps. Optimal trap size and fence length for a standardized trap mouth was determined by comparing the total species richness sampled when the accumulated circumference was approximately 206 cm. This value was chosen as it represented the maximum number of traps available (15) with a diameter of 4.3 cm. Nine 7.0 cm traps and six 11.1 cm traps were needed at this value. The trap size/fence length combination maximizing species richness at this intensity was considered optimal.

The optimal combination for a standardized fence length was determined by comparing the total species richness sampled when the accumulated length of fence used for those traps with fences was 24 m. This required 12 traps with 2 m fences, six traps with 4 m fences and four traps with 6 m fences. The combination sampling the highest species richness was considered optimal.

The optimal combination for a standardized handling time was that giving the highest species richness within a given period. Handling time for a single trap from each trap size was calculated by summing the mean of the following time measurements: dig in trap and install the fence (if appropriate); pour the trapping solution; set the trap; and collect the trap. Mean handling time represented five repetitions of each task. Cumulative handling times for increasing numbers of traps was calculated by multiplying the mean handling time for each combination by the number of traps used. Standardization of handling time was achieved when the accumulated handling time was approximately 23 minutes and 50 seconds. This value represented the maximum period that utilized all 15 traps for the most efficient trap size/fence length combination.

RESULTS

Pitfall trapping resulted in the capture of 610 adult spiders, representing 24 families and 63 species. As expected, increasing trap size and/or increasing fence length resulted in greater captures of spiders.

Univariate analysis.—For our full data set, ANOVAs revealed differences in mean spider abundance, plus family and species richness for trap size, fence length, and location (Table 1; Figs. 1–4). No significant interaction effects were found between the factors FENCE, TRAP and LOCATION.

Comparisons of means revealed traps with fences collected significantly higher abundances and more families and species than traps without fences (Figs. 1–4; Table 2). Also, traps with 6 m fences were significantly greater in these variables than traps with 2 m fences. All trap diameters were found to differ significantly from each other for family and species richness, but not abundance. Significantly increases in abundance were found only when trap diameter was increased from 4 to 11.1 cm and from 7 to 11.1 cm (Figs. 1–4; Table 2).

When individual fence lengths were considered separately in their own data subsets, the largest trap size always resulted in more species being caught. No significant interactions were found between TRAP and LOCATION (Table 3). For 2 m fences, 11.1 cm diameter traps caught more species than 4.3 cm traps (Fig. 5; Table 4). For 4 m fences, 11.1 cm diameter traps caught more species than 4.3 or 7.0 cm traps (Fig. 6; Table 4). For 6 m

Table 1.—F-ratios and significance levels from three-way ANOVAs of TRAP, FENCE and LOCATION on transformed spider variables for the full data set. Bold text denotes statistically significant difference at *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$; ^denotes non-significant trend at $P < 0.1$.

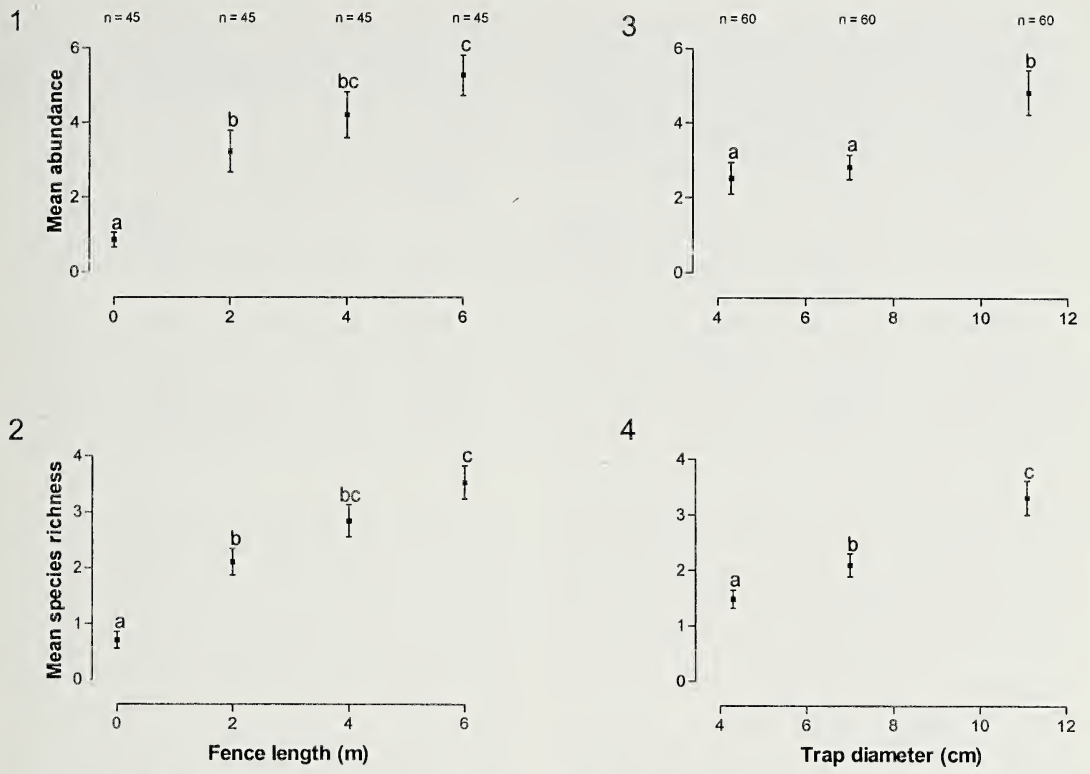
		Effects						
Data set	Dependent variables	FENCE × TRAP × LOCATION d.f. 12, 144	FENCE × TRAP d.f. 6, 144	FENCE × LOCATION d.f. 6, 144	TRAP × LOCATION d.f. 4, 144	FENCE d.f. 3, 144	TRAP d.f. 2, 144	LOCATION d.f. 2, 144
Full data set	Abundance	1.549	0.816	1.786	0.732	**39.171*** **	**14.171*** **	**14.277*** **
	Family richness	1.285	0.648	1.351	0.325	**34.347*** **	**18.095*** **	**4.146**^
	Species richness	1.471	0.881	1.912^	0.684	**39.885*** **	**23.161*** **	**6.259****

fences, 11.1 cm diameter traps also caught more species than 4.3 cm traps (Fig. 7; Table 4). Unlike the full data set, however, no data subsets showed a significant increase in species richness as trap size increased from 4.3–7.0 cm diameter (Table 4).

Traps with fences caught more species of spiders for each individual trap size when fence length was examined separately in individual data subsets for the 4.3 cm and 11.1 cm diameter traps (Figs. 8–9). Unlike the full data set, no significant difference in species richness occurred between the 2 m and 6 m fences for 11.1 cm traps (Table 4). No significant interactions were found between FENCE and LOCATION for these data (Table 3). For the 7.0 cm diameter traps data subset a significant interaction occurred between the factors FENCE and LOCATION. We do not consider it further.

Multivariate analysis.—The taxonomic composition of spider species collected was quite similar between some trap diameter/fence length combinations (similarity > 60 %). Yet, between others, similarity was low (< 25 %). Multidimensional scaling permitted us to represent these similarities adequately in two-dimensional ordination space with a relatively low amount of distortion, stress < or = 0.1 (Figs. 10–11). Similar results were obtained with hierarchical clustering (Fig. 12).

Fenced vs. unfenced: The addition of a fence caused a marked alteration in species composition. MDS showed all traps with fences to cluster loosely together, and apart from traps without fences (Fig. 10). Similarly, hierarchical clustering showed fenced traps to form a terminal branch (Fig. 12). ANOSIM confirmed that when combined, traps without fences were significantly different in species composition to traps with fences, (unfenced vs. 2 m, 4 m and 6 m fences) (Table 5). SIMPER analysis revealed that almost 47 % of the similarity in species composition between unfenced traps with diameters of 4.3, 7.0 and 11.1 cm was attributable to a single species, *Myrmopopaea* sp. 1 (Oonopidae). This species, along with *Ambicodamus marae* (Nicodamidae) and *Longepi woodman* (Lamponidae), were also primarily responsible for almost 49 % of the similarity in species composition between fenced traps. Despite this, *Myrmopopaea* sp. 1 made only a small contribution (2.26 %) to the difference between



Figures 1–4.—Effect of increasing fence length (1, 2) and increasing trap diameter (3, 4) on spider catchability: (1, 3) abundance, and (2, 4) species richness. Different lower case letters denote significantly different means (established from post-hoc tests on transformed data, Table 2). Error bars are ± one standard error of the mean.

fenced and unfenced traps. This difference was determined by high and low abundances of many species (Table 6). Also, unfenced 7.0 and 11.1 cm traps were more similar in composition to fenced traps than unfenced 4.3 cm traps (Figs. 10, 12).

Fence length: No difference in taxonomic composition was found between any pairwise combination of traps with 2, 4 or 6 m fences. The only difference in taxonomic composition found was between fenced and unfenced traps. ANOSIMs revealed significantly differences in species composition between unfenced traps and those with 4 or 6 m fences (Tables 5, 7).

Trap diameter: When all trap diameter/fence length combinations were considered in the one analysis, no difference in taxonomic composition was found between the different trap diameters (Table 5).

Trap diameter (fenced traps only): For fenced traps, trap diameter, rather than fence length, appeared to be the primary factor influencing similarity in taxonomic composition. Hierarchical clustering revealed that 4.3 cm fenced traps formed a terminal branch, as did fenced traps with 11.1 cm diameters (Fig. 12). With unfenced traps excluded, ANOSIMs revealed significant differences in species composition between pairwise combinations of trap sizes (4.3 cm vs. 7.0 cm vs. 11.1 cm diameter) (Tables 5, 7). SIMPER analysis revealed >11 species contributed to the first 50 % of the difference in taxonomic composition between all combinations, with no individual species contributing more than 6.9 % (Table 8).

Effect of trap diameter and fence length at higher taxonomic levels: The results outlined above for species were generally maintained when we repeated our analysis at familial rank. In fact, MDS ordinations obtained at species and family ranks were remarkably similar (Figs. 10 vs. 11). Testing between underlying similarity matrices with the Mantel's test confirmed both were significantly similar

Table 2.—Mean differences obtained from *post-hoc* means comparisons using Scheffé's S for TRAP and FENCE on transformed spider variables for the full data set. Bold text denotes statistically significant difference of *** $P < 0.001$, ** $P < 0.01$ or * $P < 0.05$. TD4 denotes trap diameter 4.3 cm, TD7 denotes trap diameter 7.0 cm, TD11 denotes trap diameter 11.1 cm, FL0 denotes no fence, FL2 denotes 2 m fence, FL4 denotes 4 m fence, FL6 denotes 6 m fence.

	Effects								
	FENCE						TRAP		
Dependent variables	FL0 vs. FL2	FL0 vs. FL4	FL0 vs. FL6	FL2 vs. FL4	FL2 vs. FL6	FL4 vs. FL6	TD4 vs. TD7	TD4 vs. TD11	TD7 vs. TD11
Abundance	**0.71*** **	**0.96*** **	**1.23*** **	0.25	**0.52*** **	0.27	0.17	**0.54*** **	**0.37** **
Family richness	**0.47*** **	**0.65*** **	**0.85*** **	0.18	**0.37** **	0.20	**0.20***	**0.45*** **	**0.26** **
Species richness	**0.51*** **	**0.72*** **	**0.92*** **	0.21	**0.41*** **	0.20	**0.20***	**0.52*** **	**0.32*** **

(sample statistic Rho = 0.879; permuted statistics > Rho = 0; $P < 0.001$). The result of the ANOSIMs reported above at species level also remained unchanged at family rank. The only changed result was in the structuring of 7.0 and 11.1 cm traps with fences in the hierarchical clustering dendrogram.

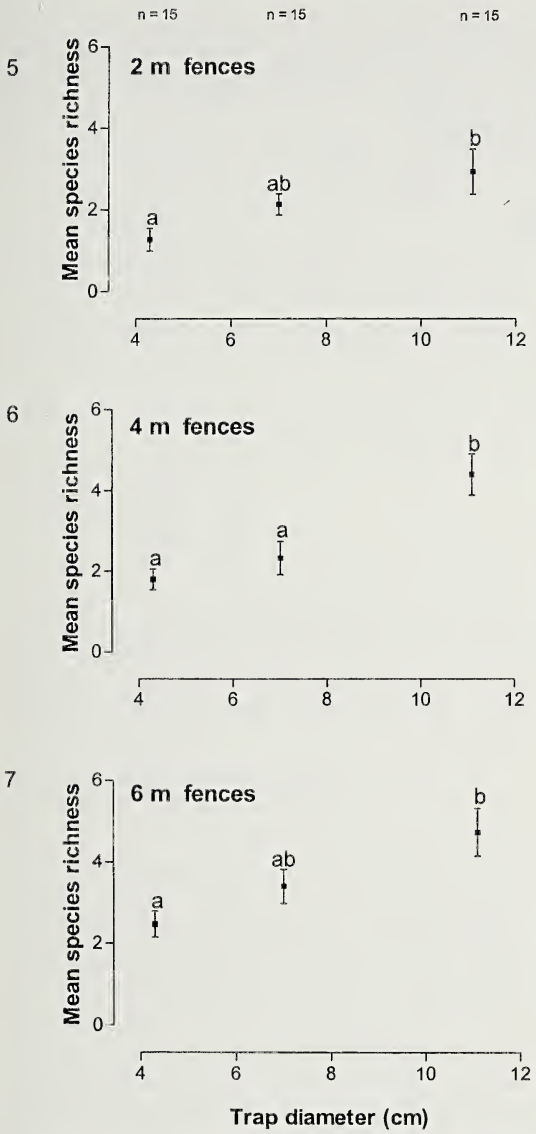
Determination of an optimal combination of trap size/fence length.—Smoothed species accumulation curves for increasing numbers of traps revealed that different trap size/fence length combinations accrued species at different rates. Fenced traps accumulated species more rapidly than unfenced traps (Fig. 13). Moreover, for each trap size, longer fences accrued species more rapidly. Additionally, species were still being accumulated for all combinations of trap size/fence length as no curves had reached an asymptote (Fig. 13).

Standardized number of traps: Standardizing at 15 traps revealed large differences in the number of species collected by each trap size/fence length combination (Fig. 13). At 15 traps, 4.3 cm unfenced traps caught only five species, whereas 11.1 cm traps with fences of 4 m or greater collected more than 30 species. Traps with fences generally caught more species than traps without fences. The only exception was the 4.3 cm trap with a 2 m fence, which caught only 10 species compared to the 12 species collected by the 11.1 cm unfenced trap. The 11.1 cm traps with 4 or 6 m fences were considered optimal for a standardized number of traps.

Standardized trap circumference: Standardizing at a cumulative circumference also revealed large differences in the number of species collected by each trap size/fence length combination (Fig. 14). Unfenced traps caught < six species compared to > 10 for fenced traps. Traps with long fences were optimal for this criterion. All traps with 6 m fences and

Table 3.—F-ratios and significance levels from two-way ANOVAs of TRAP and LOCATION or FENCE and LOCATION on transformed spider species richness for data subsets. Bold text denotes statistically significant difference at *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

	Effects				
Data subset	FENCE × LOCATION d.f. 6, 144	TRAP × LOCATION d.f. 4, 144	FENCE d.f. 3, 144	TRAP d.f. 2, 144	LOCATION d.f. 2, 144
Small traps (4.3 cm diameter)	0.994	—	**10.951*** **	—	1.179
Medium traps (7 cm diameter)	**3.567** **	—	—	—	—
Large traps (11.1 cm diameter)	1.120	—	**12.578*** **	—	2.307
Short fences (2 m)	—	1.064	—	**4.498*** **	1.869
Medium fences (4 m)	—	2.257	—	**11.711*** **	**4.056***
Long fences (6 m)	—	0.337	—	**6.297** **	**4.241***



Figures 5–7.—Effect of increasing trap diameter on spider species richness for fenced traps with: (5) short fences of 2 m, (6) medium fences of 4 m, or (7) long fences of 6 m. Different lower case letters denote significantly different means (established from *post-hoc* tests on transformed data, Table 4). Error bars are ± one standard error of the mean.

the 11.1 cm diameter trap with a 4 m fence collected high numbers of species (> 16).

Standardized fence length: For fenced traps, standardizing at a cumulative fence length of 24 m revealed large traps generally collected more species. All 11.1 cm traps collected > 13 species, whereas most 7.0 cm and all 4.3 cm diameter traps caught fewer than 11 species (Fig. 15). That said, when each trap diameter was considered separately, and traps were ranked by the number of species collected, traps with 2 m fences always collected the most species (Fig. 15).

Standardized handling time: Standardizing for handling time revealed very different results compared to a standardized number of traps or trap circumference. All traps collected very similar numbers of species (Fig. 16), despite mean handling times differing for each trap size/fence length combination (Table 9). Overall, the 11.1 cm trap with a 4 m fence was optimal, as it could be expected to collect more species than all other traps (>13), during the standardized handling period (Fig. 16). Other subtle differences between trap size/fence length combinations were evident. Firstly, the number of species expected to be collected increased with trap size. Between four to six species were collected from 4.3 cm diameter traps. Six to nine species were caught by 7.0 cm traps. The most species were collected by 11.1 cm traps (8 to 14). Secondly, when each trap size was considered separately, and traps were ranked by the number of species collected, traps with 6 m fences always collected the least.

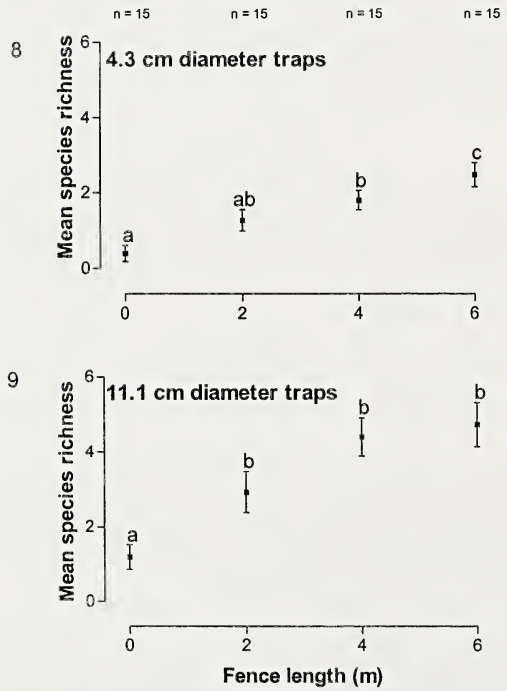
DISCUSSION

Does adding fences to pitfall traps increase spider catchability in Western Australian jarrah forest?—We found fenced traps caught greater abundance of individuals and more spider families, and species in this habitat. These findings support earlier research in the monsoonal tropics of northern Australia where increased abundances of spiders and dominant taxa were captured in fenced traps compared to unfenced traps (Churchill unpub. data). It is important, however, that the role of trap diameter and fence design be tested in other habitats and over different periods and seasons.

To date, fenced traps have not been widely used to sample spiders. However, they are used frequently to sample amphibians, reptiles and small mammals (Blomberg & Shine 1996; Halliday 1996). For vertebrates, fences increased abundance and species richness of animals collected (Bury & Corn 1987; Morton et al. 1988; Friend et al. 1989), but see Williams & Braun (1983). For invertebrates other than spiders, fenced traps are uncommon. In-

Table 4.—Mean differences obtained from *post-hoc* means comparisons using Scheffé's *S* for TRAP and FENCE on transformed spider species richness for data subsets. Bold text denotes statistically significant difference of *** $P < 0.001$, ** $P < 0.01$ or * $P < 0.05$. TD4 denotes trap diameter 4.3 cm, TD7 denotes trap diameter 7.0 cm, TD11 denotes trap diameter 11.1 cm, FL0 denotes no fence, FL2 denotes 2 m fence, FL4 denotes 4 m fence, FL6 denotes 6 m fence.

	Effects								
	FENCE						TRAP		
Data subset	FL0 vs. FL2	FL0 vs. FL4	FL0 vs. FL6	FL2 vs. FL4	FL2 vs. FL6	FL4 vs. FL6	TD4 vs. TD7	TD4 vs. TD11	TD7 vs. TD11
Small traps (4.3 cm diameter)	0.37	**0.58****	**0.79*****	0.21	**0.42***	0.21	—	—	—
Large traps (11.1 cm diameter)	**0.54***	**0.95*****	**1.02*****	0.40	0.47	0.00	—	—	—
Short fences (2 m)	—	—	—	—	—	—	0.33	**0.50***	0.17
Medium fences (4 m)	—	—	—	—	—	—	0.14	**0.69*****	**0.55****
Long fences (6 m)	—	—	—	—	—	—	0.25	**0.56****	0.30



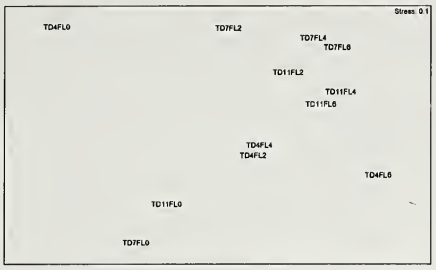
Figures 8–9.—Effect of fencing length on spider species richness for: (8) small traps (4.3 cm diameter), or (9) large traps (11.1 cm diameter). Different lower case letters denote significantly different means (established from post-hoc tests on transformed data, Table 4). Error bars are ± one standard error of the mean.

creases in abundance and species richness of beetles collected with fenced traps, however, have been documented (Durkis & Reeves 1982; Morrill et al. 1990; Crist & Wiens 1995).

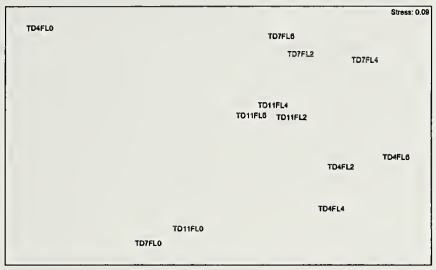
Our study revealed marked differences in taxonomic composition between fenced and unfenced traps. This may have arisen because pitfall traps preferentially sample species moving actively across the ground surface. Adding fences my skew this bias further towards the most active species. It will be these species most likely to encounter fences and, by following the fence, fall into the trap. For example, SIMPER analysis revealed the nicodamid *Ambicodamus marae* made the highest contribution to the dissimilarity between fences and unfenced traps. This species had a mean abundance of 5.22 across fenced traps but was not collected at all in unfenced traps (Table 7). Given that of the 47 individuals collected, 45 were adult males, it is likely that at the time of our sampling, males were actively searching for mates thus leading to high captures in fenced traps. Similar results of species-specific differences in catchability between unfenced traps and fenced traps have been documented for beetles (Morrill et al. 1990).

How does trap size influence spider catchability for fenced and unfenced traps?—Generally, higher abundances and more species were collected as trap size increased, however, differences between each

10



11



Figures 10–11.—Ordinations showing similarity in spider community composition between each fence length/trap size combination at (10) species and (11) family ranks. TD4 denotes trap diameter 4.3 cm, TD7 denotes trap diameter 7.0 cm, TD11 denotes trap diameter 11.1 cm, FL0 denotes no fence, FL2 denotes 2 m fence, FL4 denotes 4 m fence, FL6 denotes 6 m fence.

trap size were not always present (Figs. 3–7). Absent in the fenced 2 and 6 m data subsets, but present in the full dataset, were significant differences between 4.3 versus 7.0 cm traps, and between 7.0 versus 11.1 cm traps. Removal of significant differences most likely arose through a loss of power associated with fewer replicates. Greater captures from large pitfall traps with fences compared to small pitfall traps with fences has been found also for reptiles (Morton et al. 1988).

For fenced traps, the primary factor influencing taxonomic composition was trap size; fence length had no significant effect. ANOSIMs revealed significant differences between each trap size for fenced traps, but no differences between traps with 2, 4 or 6 m fences. Reasons behind differences in taxonomic composition between trap sizes for fenced traps are not obvious. They arose from combined contribution of subtle differences in the abundances of many species, rather than a limited few. Some species were preferentially collected in smaller traps. For example, Salticidae Genus 9 sp. 01 was collected in high abundance in 4.3 cm traps, intermediate abundance in 7.0 cm traps and in low abundance in 11.1 cm traps (Table 9). Conversely, other species such as *Ambicodamus marae*, were biased against 4.3 cm traps, but didn't discriminate between 7.0 or 11.1 cm traps. Finally, some species were captured predominantly in intermediate sized 7.0 cm traps (e.g. *Hestimodema* sp. 02 and *Myrmopopaea* sp. 01). Other species were biased against this trap size (e.g. Salticidae Genus 3 sp. 02). We interpret these findings as arising from species-specific differences in behavior that preferentially predisposed individual species to capture (or prevented escape) by each individual trap size.

For unfenced traps, even for very small sample sizes, trap diameter can have a major influence on spider abundance and species richness. Our earlier findings revealed greater captures with increasing trap size when we compared 4.3, 7.0, 11.1 and 17.1 cm diameter traps (Brennan et al. 1999). In particular, mean abundance and species richness differed significantly between the three largest traps. For other invertebrates, size of unfenced traps can also influence captures. Larger traps have yielded greater abundance and species richness of ants and beetles (Luff 1975; Abensperg-Traun & Steven 1995). However, for both groups trap size influenced taxonomic composition. For example, small trap sizes preferentially sampled small beetles and large traps were better for large species (Luff 1975). Similar results were obtained in the present study. Spider taxonomic composition differed markedly between unfenced 4.3 cm versus unfenced 7.0 and 11.1 cm diameter traps. The later trap sizes clustered together tightly in ordinations.

The above finding highlights the difficulties of making valid comparisons between studies using different sampling protocols. Here we can but echo earlier calls for arachnologists to standardize sampling protocols thereby permitting more valid comparisons to be made (Coddington et al. 1991; Churchill 1993; New 1999).

How does fence length influence spider catchability for fenced traps?—Increasing fence length yielded increased spider abundance plus the richness of families and species in our full data set. In fact, traps with 6 m fences had greater captures than those with 2 m fences for all of these variables. Greatest

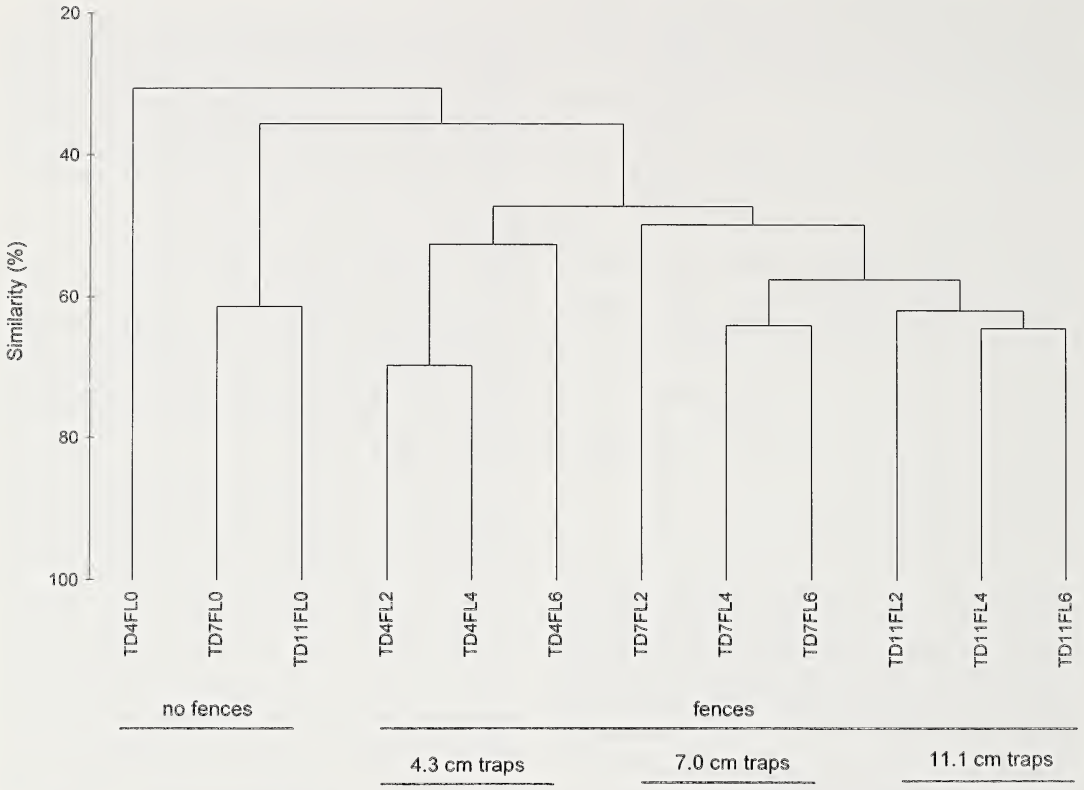


Figure 12.—Dendrogram for hierarchical clustering (group-average linking) of similarity in spider species composition between each fence length/trap size combination.

increases, however, occurred between unfenced traps and those with 2 m fences (our smallest length of fence). Given these findings, two questions arise. Firstly, what is the minimum length of fence required to derive the initial rapid increase in captures? Secondly, at what length of fence will no additional benefit be gained by adding more fence? The former cannot be answered from our dataset. We suggest future workers test the effectiveness of fences over a wider range of lengths. These should include very short fences of perhaps only 10 to 20 cm (5 to 10 cm each side of the trap). With respect to the second question, our results differed between data sets.

When fence length was considered separately in data subsets for 4.3 and 11.1 cm diameter traps, the rate of increase in species

Table 5.—ANOSIM global test results for difference in species composition between various combinations of trap diameter and fence lengths. Bold text denotes statistically significant differences in taxonomic composition at ** $P < 0.01$ or * $P < 0.05$. [a] denotes all possible permutations used. TD4 denotes trap diameter 4.3 cm, TD7 denotes trap diameter 7.0 cm, TD11 denotes trap diameter 11.1 cm, FL0 denotes no fence, FL2 denotes 2 m fence, FL4 denotes 4 m fence, FL6 denotes 6 m fence.

Data set used	Factors	Global R	Permutations available	Permuted statistics > global R
All trap/fence combinations	FL0 vs. FL2 & FL4 & FL6	0.871	220[a]	**1****
	FL0 vs. FL2 vs. FL4 vs. FL6	0.309	15400[a]	**378***
	TD4 vs. TD7 vs. TD11	0.1	5775[a]	1114
Fenced traps only	TD4 vs. TD7 vs. TD11	0.712	280[a]	**1****

Table 6.—Individual species contributions to the difference in taxonomic composition between fenced and unfenced traps (average dissimilarity = 66.39%), from SIMPER analysis of root transformed standardized data.

Species	Mean abundance		Mean dissimilarity	Contribution (%)	Cumulative contribution (%)
	Unfenced	Fenced			
Ambicodamus marae Harvey 1995	0.00	55.22	4.24	6.38	6.38
Linyphiidae Genus 02 sp. 02	1.33	1.00	3.96	5.96	12.34
Longepi woodman Platnick 2000	0.00	3.89	3.57	5.38	17.73
Supunna funerea Simon 1896	1.33	0.67	3.30	4.97	22.69
Anapidae Genus 01 sp. 02	0.00	2.33	3.04	4.58	27.28
Tasmanoonops sp. 02	0.67	0.44	3.04	4.57	31.85
Hestimodema sp. 02	0.33	2.89	2.82	4.24	36.10
Gnaphosidae Genus 01 sp. 01	0.67	1.67	2.77	4.17	40.27
Elassoctenus sp. 03	0.67	0.22	2.77	4.17	44.44
Salticidae Genus 03 sp. 02	0.67	4.56	2.38	3.58	48.02

richness for additional units of fence differed (Figs. 8 vs. 9). The 4.3 cm diameter traps followed the pattern noted previously in the full data set. Additional increments of fences increased the catch so that traps with 6 m fences had significantly more than those with 2 m fences. Conversely, for 11.1 cm traps no further significant increase in species richness occurred with 4 or 6 m fencing.

For beetles, increasing fence length yields greater abundance. Durkis and Reeves (1982) compared unfenced traps to traps with fences of 0.3, 0.9 or 1.5 m. They found 1.5 m fences collected more beetles than traps with 0.9 m fences and these lengths were superior to 0.3 m fences or unfenced traps (Durkis & Reeves 1982). Other authors report variable effects. Morrill et al. (1990) compared unfenced traps and traps with fences of 0.05, 0.10 or 0.15 m. For some carabid species, abundance did not differ between fenced and unfenced traps. For other species, 0.20 m fences were superior to 0.05 m fences.

For vertebrates, increasing fence length has often been accompanied by increased captures, even for very long fences (Bury & Corn 1987; Friend et al. 1989; Hobbs et al. 1994). Hobbs et al. (1994) reported increased reptile

Table 7.—ANOSIM pairwise tests results for of differences in species composition between various combinations of trap diameter and fence lengths. [a] denotes all possible permutations used. [b] denotes level of statistical significance (P) was set at 0.1 owing to the low number of permutations available. Bold text denotes statistically significant differences in taxonomic composition at * $P = 0.1$. TD4 denotes trap diameter 4.3 cm, TD7 denotes trap diameter 7.0 cm, TD11 denotes trap diameter 11.1 cm, FL0 denotes no fence, FL2 denotes 2 m fence, FL4 denotes 4 m fence, FL6 denotes 6 m fence.

Data set used	Factors and pairwise tests of factor levels	R statistic	Permutations available	Permuted statistics > R statistic
All trap/fence combinations	FL0 vs. FL2 vs. FL4 vs. FL6			
	FL0 vs. FL2	0.481	10^{ab}	2
	FL0 vs. FL4	0.778	10^{ab}	**1***
	FL0 vs. FL6	0.741	10^{ab}	**1***
	FL2 vs. FL4	−0.185	10^{ab}	8
	FL2 vs. FL6	0.074	10^{ab}	4
	FL4 vs. FL6	−0.111	10^{ab}	8
Fenced traps only	TD4 vs. TD7 vs. TD11			
	TD4 vs. TD7	0.741	10^{ab}	**1***
	TD4 vs. TD11	0.926	10^{ab}	**1***
	TD7 vs. TD11	0.519	10^{ab}	**1***

Table 8.—Individual species contributions to differences in taxonomic composition between different trap sizes amongst traps with fences, from SIMPER analysis of root transformed standardized data. TD4 denotes trap diameter 4.3 cm, TD7 denotes trap diameter 7.0 cm, TD11 denotes trap diameter 11.1 cm.

Pairwise comparison	Species	Mean abundance			Mean dissimilarity	Contribution (%)	Cumulative contribution (%)
		TD4	TD7	TD11			
TD4 vs. TD7 (average dissimilarity = 53.17%)	*Hestimodema* sp. 02	0.33	5.67	—	3.67	6.90	6.90
	Gnaphosidae Genus 01 sp. 01	3.00	0.00	—	3.60	6.78	13.67
	Lycidas michaelseni (Simon 1909)	0.00	2.33	—	2.32	4.36	18.03
	Myrmopopaea sp. 01	23.00	14.33	—	2.27	4.27	22.30
	Salticidae Genus 03 sp. 02	4.67	2.67	—	2.26	4.24	26.54
	Ambicodamus marae Harvey 1995	1.33	5.67	—	2.17	4.07	30.61
	Elassoctenus sp. 01	0.33	2.00	—	1.92	3.61	34.22
	Linyphiidae Genus 02 sp. 02	0.00	1.33	—	1.90	3.57	37.80
	Zodariidae Genus 01 sp. 02	0.33	1.33	—	1.80	3.38	41.17
	Longepi woodman Platnick 2000	1.33	4.67	—	1.78	3.35	44.53
	Salticidae Genus 09 sp. 01	1.00	0.33	—	1.78	3.35	47.88
	Opopaea sp. 01	1.67	1.33	—	1.52	2.85	50.73
TD4 vs. TD11 (average dissimilarity = 52.39%)	Anapidae Genus 01 sp. 02	4.00	—	0.67	2.74	5.23	5.23
	Gnaphosidae Genus 01 sp. 01	3.00	—	2.00	2.73	5.21	10.44
	Lycidas michaelseni (Simon 1909)	0.00	—	4.00	2.71	5.16	15.60
	Gnaphosidae Genus 01 sp. 02	0.00	—	2.33	2.14	4.09	19.69
	Lycidas sp. 04	0.33	—	3.67	1.98	3.79	23.48
	Salticidae Genus 09 sp. 01	1.00	—	0.00	1.88	3.59	27.07
	Linyphiidae Genus 02 sp. 02	0.00	—	1.67	1.83	3.49	30.56
	Ambicodamus marae Harvey 1995	1.33	—	8.67	1.80	3.44	34.00
	Hestimodema sp. 02	0.33	—	2.67	1.77	3.37	37.37
	Tasmanoonops sp. 03	0.00	—	1.33	1.59	3.04	40.41
	Myrmopopaea sp. 01	23.0	—	29.0	1.56	2.98	43.39
	Tasmanoonops sp. 02	0.67	—	0.67	1.35	2.59	45.98
	Longepi woodman Platnick 2000	1.33	—	5.67	1.20	2.30	48.27
	Elassoctenus sp. 01	0.33	—	1.00	1.19	2.26	50.54
TD7 vs. TD11 (average dissimilarity = 45.83%)	Gnaphosidae Genus 01 sp. 02	—	0.00	2.33	1.98	4.32	4.32
	Zodariidae Genus 01 sp. 02	—	1.33	0.00	1.94	4.24	8.56
	Hestimodema sp. 02	—	5.67	2.67	1.63	3.55	12.11
	Salticidae Genus 03 sp. 02	—	2.67	6.33	1.58	3.44	15.55
	Anapidae Genus 01 sp. 02	—	2.33	0.67	1.55	3.39	18.93
	Elassoctenus sp. 01	—	2.00	1.00	1.50	3.28	22.22
	Supunna funerea Simon 1896	—	0.00	1.33	1.47	3.21	25.43
	Myrmopopaea sp. 01	—	14.33	29.00	1.38	3.01	28.44
	Gnaphosidae Genus 01 sp. 01	—	0.00	2.00	1.35	2.95	31.39
	Longepi woodman Platnick 2000	—	4.67	5.67	1.33	2.90	34.28
	Lycidas michaelseni (Simon 1909)	—	2.33	4.00	1.29	2.82	37.11
	Opopaea sp. 01	—	1.33	2.33	1.17	2.54	39.65
	Gamasomorpha sp. 02	—	0.00	1.33	1.08	2.36	42.02
	Tasmanoonops sp. 03	—	0.33	1.33	1.06	2.32	44.34
	Linyphiidae Genus 02 sp. 02	—	1.33	1.67	1.04	2.27	46.61
	Lampona brevipes L. Koch 1872	—	0.67	0.00	1.04	2.26	48.87
	Australobus sp. 01	—	1.00	1.33	0.99	2.16	51.04

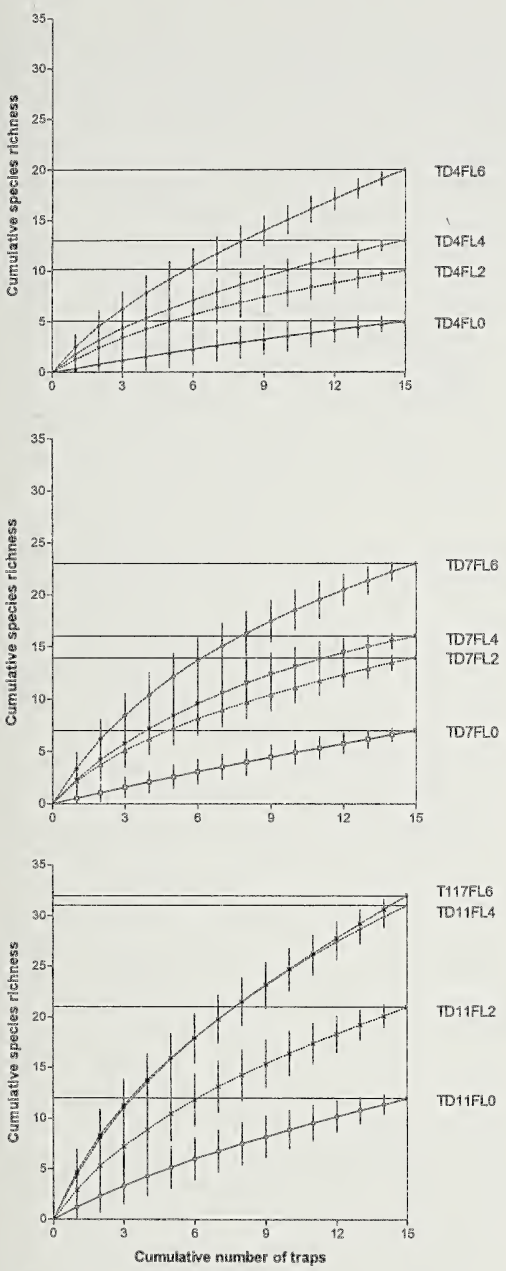


Figure 13.—Smoothed species accumulation curves showing the number of species likely to be sampled with standardized number of traps (15 traps) for each fence length/trap size combination. Error bars are ± one standard deviation of the mean. TD4 denotes trap diameter 4.3 cm, TD7 denotes trap diameter 7.0 cm, TD11 denotes trap diameter 11.1 cm, FL0 denotes no fence, FL2 denotes 2 m fence, FL4 denotes 4 m fence, FL6 denotes 6 m fence. Curves are spread over three graphs for the purpose of clarity.

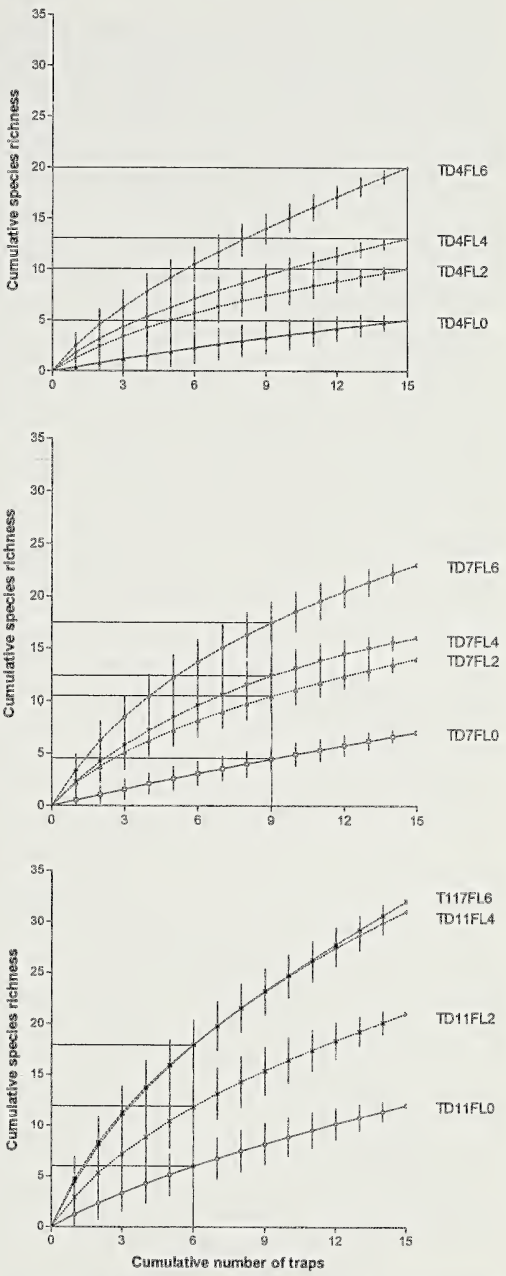


Figure 14.—Smoothed species accumulation curves showing the number of species likely to be sampled with standardized cumulative trap circumference of 206 cm for each fence length/trap size combination. Error bars are ± one standard deviation of the mean. TD4 denotes trap diameter 4.3 cm, TD7 denotes trap diameter 7.0 cm, TD11 denotes trap diameter 11.1 cm, FL0 denotes no fence, FL2 denotes 2 m fence, FL4 denotes 4 m fence, FL6 denotes 6 m fence. Curves are spread over three graphs for the purpose of clarity.

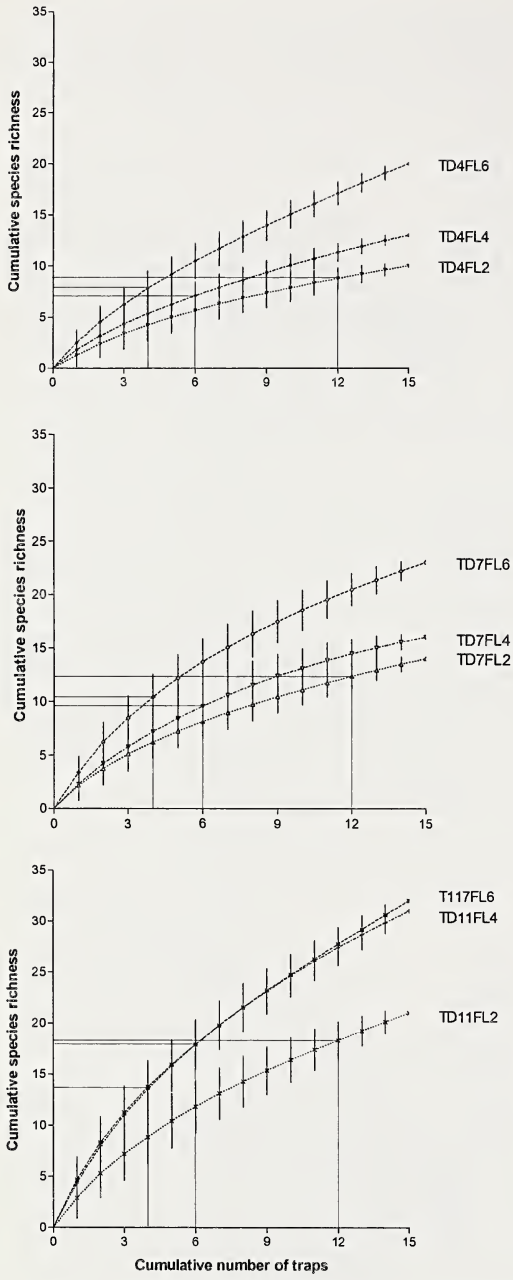


Figure 15.—Smoothed species accumulation curves showing the number of species likely to be sampled with standardized cumulative fence length of 24 m for all trap sizes of fenced traps. Error bars are ± one standard deviation of the mean. TD4 denotes trap diameter 4.3 cm, TD7 denotes trap diameter 7.0 cm, TD11 denotes trap diameter 11.1 cm, FL2 denotes 2 m fence, FL4 denotes 4 m fence, FL6 denotes 6 m fence. Curves are spread over three graphs for the purpose of clarity.

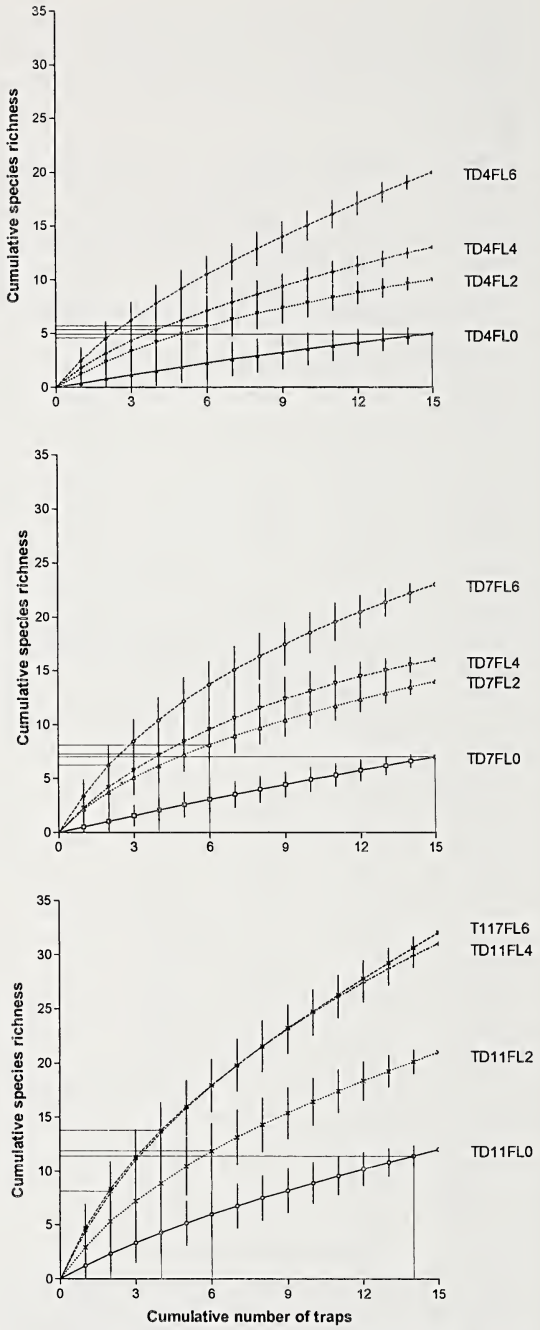


Figure 16.—Smoothed species accumulation curves showing the number of species likely to be sampled with standardized handling time of approximately 23 minutes and 50 seconds for each fence length/trap size combination. Error bars are ± one standard deviation of the mean. TD4 denotes trap diameter 4.3 cm, TD7 denotes trap diameter 7.0 cm, TD11 denotes trap diameter 11.1 cm, FL0 denotes no fence, FL2 denotes 2 m fence, FL4 denotes 4 m fence, FL6 denotes 6 m fence. Curves are spread over three graphs for the purpose of clarity.

captures with 66 m as opposed to 50 m fences. However, Williams and Braun (1983) found no difference in small mammal captures between traps with 0.6 or 1.2 m fences.

Although not the focus of this study, trap location was important for 7.0 cm diameter traps. A significant interaction effect was found between FENCE and LOCATION for species richness (Table 3). This result may have arisen through differences in habitat structure or the influence of trap spacing. Differences in trap arrangement and spacing can influence the abundance, species richness and composition of beetles (Crist & Wiens 1995; Digweed et al. 1995; Ward et al. 2001). The role of trap arrangement and spacing for spiders should be investigated.

Determination of an optimum combination of trap diameter and fence length.—Our results show clearly that some trap diameter/fence length combinations are more efficient than others. For example, results for a standardized fence length suggest that if a total of only 24 m of fence were available, more species might be collected in 12 traps with 2 m fences than in four traps with 6 m fences. This finding is in conflict with Bury and Corn's (1987) statement that "ultimately, the total amount of fence in a [forest] stand is probably more important than individual lengths." It is important to note, however, that in our study the best trap diameter/fence length combination often varied with the efficiency criterion used. For handling time, 11.1 cm trap with a 4 m fence were best. That said, unfenced traps often were very similar in efficiency to fenced traps. This suggests that at our study site during our sampling period, when pitfall trapping with 11.1 cm traps, fieldworkers would be equally justified digging in just six traps with a 2 m fence or 14 unfenced traps. Given this choice, we would much prefer to dig in many unfenced traps for the following reasons. Firstly, although duration of the tasks is similar, digging in many unfenced traps requires much less strenuous physical effort. Secondly, digging in fences causes considerably more physical disturbance and alteration of habitat surrounding the trap. Thirdly, we suspect unfenced traps require less maintenance. As part of a two-year monitoring program of jarrah forest spiders, we have sampled at three monthly intervals using fenced and unfenced traps. Fences have needed repairing constantly owing to disturbance by kangaroos and feral pigs. Branches and twigs falling on fences also have increased the time required to maintain fenced traps in good condition. Fourthly, fences may potentially bias captures by hindering locomotion or changing microhabitats as litter and debris accumulates against them more rapidly than other areas surrounding the trap. Consequently, using drift-fences over many years may allow microhabitats surrounding traps to change more rapidly than traps without fences. For our monitoring program, any litter than had built up against fences was redistributed a week prior to opening the traps. Finally, fences have the potential to inhibit perception of internal spatial heterogeneity within spider communities within a study site. Consolidating individuals from a wider spatial area into a single fenced trap removes patchiness in the occurrence of individuals that would be evident in multiple unfenced traps.

Could other fence designs be more efficient?—The fenced traps we used were single pitfall traps placed in the middle of a straight fence. However, other fence designs exist. The main variations are multiple fences per trap or multiple traps per fence. In the former, a common design is to erect a second fence perpendicular to the first, so that the two fences form a cross with the pitfall trap in the centre. Morrill et al. (1990) found adding a second fence yielded higher captures only for one beetle species. Morton et al. (1988) suspected that adding a second fence was beneficial to increase reptile catch, but their results were inconclusive. Hobbs et al. (1994) showed unequivocally that adding a second fence did not increase reptile captures, despite the extra labor and length of fencing involved. That said, the latter two studies used multiple traps along one or both fences.

With respect to multiple traps per fence designs, perhaps the most common is a straight row of three or more pitfall traps connected by a single straight fence. The success of this design in relation to multiple unfenced traps for spiders has been demonstrated by Churchill (unpub. data) and was discussed previously. How this trap design compares to the simple fenced trap we used is unknown. For small mammals, amphibians and reptiles, however, Friend et al. (1989) found independent traps collected more animals than a mul-

Table 9.—Mean (± S.E.) time periods (minutes:seconds) taken to perform various pitfall trapping activities for different combinations of fence length/trap size.

Activity	Trap/fence combination					
	Fence length (m)					
	0			2		
	Trap diameter (cm)					
	4.3	7.0	11.1	4.3	7.0	11.1
Digging in traps/ fences	0:40 ± 0:02	0:40 ± 0:01	0:44 ± 0:01	3:01 ± 0:07	3:16 ± 0:07	3:11 ± 0:11
Pouring solution into traps	0:10 ± 0:00	0:11 ± 0:00	0:14 ± 0:00	0:10 ± 0:00	0:11 ± 0:00	0:14 ± 0:00
Set traps	0:20 ± 0:00	0:20 ± 0:00	0:20 ± 0:00	0:25 ± 0:00	0:25 ± 0:00	0:25 ± 0:00
Collecting traps	0:25 ± 0:00	0:25 ± 0:00	0:25 ± 0:00	0:25 ± 0:00	0:25 ± 0:00	0:25 ± 0:00
Total	1:35 ± 0:02	1:35 ± 0:01	1:43 ± 0:01	4:01 ± 0:07	4:17 ± 0:07	4:15 ± 0:11

tiple traps per fence design. They attributed this to, firstly, independent traps sampling a wider range of microhabitats and home ranges. Secondly, animals altering their daily movement patterns to avoid the fence during periods when traps were closed. Consequently, when traps were opened, they were less susceptible to capture. Another permutation of the multiple traps per fence design is two traps at either end of a fence. Friend (1984) tested this design against a fenced trap with a single pit (of a different size) that herpetofauna could approach only from one side. Consequently, there are confounding effects and we await a more rigorous test. Theoretically, however, traps placed at either end of fences may be more efficient. There is twice the probability that an animal encountering the fence will turn and move towards a trap, yet the most time consuming component of sampling (digging in the fence) remains constant. This assumes that for an animal encountering a fence, the probability of not turning away before reaching the end of the fence, is equal between fencing types. For longer fences, the probability of following to the fence's end may decline and thereby the greater efficiency of the two-trap fence over the single-trap fence.

Different fencing materials may also influence efficiency. To date, fences have been constructed of plastic, metal roofing and flyscreen. Consequently, considerable variation may be expected in cost, longevity, and time to construct, install plus maintain fences. All may influence handling time efficiency, particularly where regular trapping is undertaken or if long periods elapse between trapping. Here we used black plastic, purchased cheaply from a hardware store on a roll. Although metal roofing was readily available, it costs more per meter, cannot be cut to size easily, and is bulky to transport. Disadvantages may be outweighed, however, if metal fences last longer, require less maintenance or facilitate greater captures. The performance of different fence materials should thus be investigated. When doing so we advocate assessing performance by a number of criteria, of which one should be maintenance/handling time.

Differences in fencing efficiency may vary also between different grades of plastics. In the monitoring program mentioned previously we have used both 100 um and 200 μm thick plastic. Longevity between thickness grades varies considerably. Thicker fences deteriorated approximately twice as rapidly as thinner fences. Thicker fences began to become brittle and pieces of fence flaked off with exposure to sunlight nine months after installation. Conversely, at the end of the monitoring program, most thinner fences did not need replacing. This is not to suggest that thinner fences did not require regular maintenance. We estimate that over the course of monitoring program, even where thin fences were initially installed, half the fences were reinstalled.

Future directions.—The results presented here show clearly that both trap size and fence length can play critical roles in determining spider catch in terms of abundance, species richness and community composition. As such comparisons to date between regions, time periods or studies where pitfall trapping protocols have differed are tenuous. Future devel-

Table 9.—Extended.

Trap/fence combination					
Fence length (m)					
4			6		
Trap diameter (cm)					
4.3	7.0	11.1	4.3	7.0	11.1
5:34 ± 0:14	5:17 ± 0:17	5:26 ± 0:10	8:42 ± 0:14	8:35 ± 0:16	8:35 ± 0:17
0:10 ± 0:00	0:11 ± 0:00	0:14 ± 0:00	0:10 ± 0:00	0:11 ± 0:00	0:14 ± 0:00
0:27 ± 0:00	0:27 ± 0:00	0:27 ± 0:00	0:29 ± 0:01	0:29 ± 0:00	0:29 ± 0:00
0:25 ± 0:00	0:25 ± 0:00	0:25 ± 0:00	0:25 ± 0:00	0:25 ± 0:00	0:25 ± 0:00
6:37 ± 0:14	6:19 ± 0:17	6:32 ± 0:10	9:46 ± 0:15	9:40 ± 0:16	9:43 ± 0:17

opments in statistical analysis may assist in negotiating some of the current plethora of biases and limits to data interpretation where protocols have differed. A more direct and potentially superior line of research, however, is the development of standardized sampling protocols for spiders. The limited resources available to inventory biodiversity require that standardized sampling protocols be highly efficient. Before adopting a standardized pitfall trapping protocol for spiders it must be firmly established that the protocol is more efficient than others in a wide variety of habitat types, and across differing temporal and spatial scales. Currently the data necessary for an informed decision as to what size, preserving solution, spatial arrangement, and duration of sampling etc. to adopt for spiders is lacking. The results presented here are an important step toward identifying the most efficient protocols for trap size and fencing. Nonetheless, studies with sufficient statistical power to determine the interplay of these and other factors in combination remain scarce. The elucidation of factors influencing pitfall trap efficiency represents a priority area for research and the development of a standardized pitfall trapping protocol a key conservation goal for arachnologists.

ACKNOWLEDGMENTS

Financial support for this research was kindly provided by Alcoa World Alumina Australia, the Minerals and Energy Research Institute of Western Australia (MERIWA), and the Department of Environmental Biology at Curtin University of Technology. For fieldwork and laboratory assistance we thank Nicholas Reygaert. For assistance in identifying specimens, we thank Mark Harvey and Julianne Waldock (Western Australian Museum), Barbara Main (University of Western Australia), plus Robert Raven and Barbara Baehr (Queensland Museum). Tracey Churchill kindly permitted us to cite her unpublished data. Tracey Churchill, Mark Harvey, Elisha Ladhams, Owen Nichols, Erich Volschenk and Julianne Waldock, provided useful discussions on many aspects of sampling with pitfall traps. For constructive criticisms that improved the manuscript we thank Thomas Crist, Paula Cushing, Robert Dunn, Maggie Hodge and an anonymous reviewer. This research was conducted whilst KECB was supported by an Australian Postgraduate Award and a MERIWA student scholarship. Access to the study site was provided by Alcoa World Alumina Australia, the Western Australian Department of Conservation and Land Management, and the Western Australian Water Corporation.

LITERATURE CITED

Abensperg-Traun M. & D. Steven. 1995. The effects of pitfall trap diameter on ant species richness (Hymenoptera: Formicidae) and species composition of the catch in a semi-arid eucalypt woodland. Australian Journal of Ecology 20: 282–287.

Adis, J. 1979. Problems of interpreting arthropod sampling with pitfall traps. Zoologischer Anzeiger Jena 202:177–184.

Agosti, D. & L.E. Alonso. 2000. The ALL protocol: A standard protocol for the collection of ground-dwelling ants. Pp. 204–206. *In* Ants: Standard

Methods for Measuring and Monitoring Biodiversity. (D. Agosti, J.D. Majer, L.E. Alonso & T.R. Schultz, eds.). Smithsonian Institution Press, Washington.

Beattie, A.J., J.D. Majer & I. Oliver. 1993. Rapid biodiversity assessment: A review. Pp. 4–14. *In* Rapid Biodiversity Assessment: Proceedings of the Biodiversity Assessment Workshop, 1993 3–4 May, 1993. (Anon., ed.). Macquarie University, Sydney.

Blomberg, S. & R. Shine. 1996. Reptiles. Pp. 218–226. *In* Ecological Census Techniques: A Handbook. (W.J. Sutherland, ed.). The Bath Press, Avon.

Bray, J.R. & J.T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27:325–349.

Brennan, K.E.C., J.D. Majer & N. Reygaert. 1999. Determination of an optimal pitfall trap size for sampling spiders in a Western Australian Jarrah forest. Journal of Insect Conservation 3:297–307.

Brennan, K.E.C. 2002. The Successional Response of Spider Communities Following the Multiple Disturbances of Mining and Burning in Western Australian Jarrah forest. Ph.D. Thesis, Department of Environmental Biology, Curtin University of Technology, Perth.

Brennan, K.E.C., M.L. Moir & J.D. Majer. 2004. Exhaustive sampling in a Southern Hemisphere global biodiversity hotspot: Inventorying species richness and assessing endemicity of the little known jarrah forest spiders. Pacific Conservation Biology 10:241–260.

Bury, R.B. & P.S. Corn. 1987. Evaluation of pitfall trapping in northwestern forests: Trap arrays with drift fences. Journal of Wildlife Management 51: 112–119.

Chappin III, F.S., E.S. Zavaleta, V.T. Eviner, R.L. Naylor, P.M. Vitousek, H.L. Reynolds, D.U. Hooper, S. Lavorel, O.E. Sala, S.E. Hobbie, M.C. Mack & S. Díaz. 2000. Consequences of changing biodiversity. Nature 405:234–242.

Churchill, T.B. 1993. Effects of sampling methods on composition of a Tasmanian coastal heathland spider assemblage. Memoirs of the Queensland Museum 33:475–481.

Churchill, T.B. & J.M. Arthur. 1999. Measuring spider richness: Effects of different sampling methods and spatial and temporal scales. Journal of Insect Conservation 3:287–295.

Churchward, H.M. & G.M. Dimmock. 1989. The soils and landforms of the northern jarrah forest. Pp. 13–22. *In* The Jarrah Forest: A Complex Mediterranean Ecosystem. (B. Dell, J.J. Havel & N. Malajczuk, eds.). Kluwer Academic Publishers, Dordrecht.

Clarke, K.R. 1993. Non-parametric multivariate analysis of changes in community structure. Australian Journal of Ecology 18:117–143.

Clarke, K.R. & R.H. Green. 1988. Statistical design and analysis for a 'biological effects' study. Marine Ecological Progress Series 46:213–226.

Coddington, J.A., C.E. Griswold, C.E. Davila, D.S. Penaranda & S.F. Larcher. 1991. Designing and testing sampling protocols to estimate biodiversity in tropical ecosystems. Pp. 44–60. *In* The Unity of Evolutionary Biology: Proceedings of the Fourth International Congress of Systematic and Evolutionary Biology. (E.C. Dudley, ed.). Dioscordes Press, Portland, Oregon, USA.

Coddington, J.A., L.H. Young & F.A. Coyle. 1996. Estimating spider species richness in a southern Appalachian cove hardwood forest. Journal of Arachnology 24:111–128.

Colwell, R.K. 1994–2000. Estimate S: Statistical estimation of species richness and shared species from samples. Version 5. http://viceroy.eeb.uconn.edu/estimates.

Colwell, R.K. & J.A. Coddington. 1995. Estimating terrestrial biodiversity through extrapolation. Pp. 101–118. *In* Biodiversity: Measurement and Estimation. (D.L. Hawksworth, ed.). Chapman and Hall, London.

Crist, T.O. & J.A. Wiens. 1995. Individual movements and estimation of population size in darkling beetles (Coleoptera: Tenebrionidae). Journal of Animal Ecology 64:733–746.

Curtis, D.J. 1980. Pitfalls in spider community studies. Journal of Arachnology 8:271–280.

Cutler, B., L.H. Grim & H.M. Kulman. 1975. A study in the summer phenology of dionychious spiders from northern Minnesota forests. Great Lakes Entomologist 8:99–104.

Day, R.W. & G.P. Quinn. 1989. Comparisons of treatments after an analysis of variance in ecology. Ecological Monographs 59:433–463.

Digweed S.C., Currie C.R., Carcamo H.A. & Spence. J.R. 1995. Digging out the "digging-in effect" of pitfall traps: Influences of depletion and disturbance on catches of ground beetles (Coleoptera: Carabidae). Pedobiologia 39:561–576.

Dobyns, J.R. 1997. Effects of sampling intensity on the collection of spider (Araneae) species and the estimation of spider species richness. Environmental Entomology 26:150–162.

Duffey, E. 1962. A population study of spiders in Limestone Grassland. Journal of Animal Ecology 31:571–599.

Duffey, E. 1972. Ecological survey and the arachnologist. Bulletin of the British Arachnological Society 2:69–82.

Durkis, T.J. & R.M. Reeves. 1982. Barriers increase efficiency of pitfall traps. Entomological News 93:8–12.

Edwards, R.L. 1993. Can the species richness of spiders be determined? Psyche 100:185–208.

Friend, G.R. 1984. Relative efficiency of two pitfall-drift fence systems for sampling small vertebrates. Australian Zoologist 21:423–432.

Friend, G.R., Smith, G.T., Mitchell, D.S. & C.R. Dickman. 1989. Influence of pitfall and drift fence design on capture rates of small vertebrates in semi-arid habitats of Western Australia. Australian Wildlife Research 16:1–10.

Gaston, K.J. & R.M. May. 1992. The taxonomy of taxonomists. Nature 356:281–282.

Gist, C.S. & J.D.A. Crossley. 1973. A method for quantifying pitfall trapping. Environmental Entomology 2:951–952.

Greenslade, P.J.M. 1964. Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). Journal of Animal Ecology 33:301–310.

Greenslade, P.J.M. 1973. Sampling ants with pitfall traps: Digging in effects. Insectes Sociaux 20: 343–353.

Gurdebeke, S. & J.-P. Maelfait. 2002. Pitfall trapping in population genetic studies: Finding the right solution. Journal of Arachnology 30:255–261.

Halliday, T.R. 1996. Amphibians. Pp. 205–217. *In* Ecological Census Techniques: A Handbook. (W.J. Sutherland, ed.). The Bath Press, Avon.

Hawksworth, D.L. 1995. The resource base for biodiversity assessment. Pp. 545–605. *In* Global Biodiversity Assessment. (V.H. Heywood, ed.). United Nations Environment Programme and Cambridge University Press, Cambridge.

Hobbs, T.J., S.R. Morton, P. Masters & K.R. Jones. 1994. Influence of pitfall-trap design on sampling of reptiles in arid spinifex grasslands. Wildlife Research 21:483–490.

Holland, J.M. & S. Smith. 1999. Sampling epigeal arthropods: An evaluation of fenced pitfall traps using mark-release-recapture and comparisons to unfenced pitfall traps in arable crops. Entomologia Experimentalis et Applicata 91:347–357.

Joosse, E.N.G. & J.M. Kapteijn. 1968. Activity stimulating phenomena caused by field disturbance in the use of pitfall traps. Oecologia 1: 385–392.

Luff, M.L. 1975. Some features influencing the efficiency of pitfall traps. Oecologia 19:345–357.

Main, B.Y. 1976. Spiders. Collins, Sydney.

Manly B.F.J. 1994. Multivariate Statistical Methods: A Primer. 2nd Edition. Chapman & Hall, London.

May, R.M. 1988. How many species are there on Earth? Science 241:1441–1449.

Melbourne, B.A. 1999. Bias in the effect of habitat structure on pitfall traps: An experimental evaluation. Australian Journal of Ecology 24:228–239.

Merrett, P. 1967. The phenology of spiders on heathland in Dorset: I. Families Atypidae, Dysderidae, Gnaphosidae, Clubionidae, Thomisidae and Salticidae. Journal of Animal Ecology 36: 363–374.

Merrett, P. 1968. The phenology of spiders on heathland in Dorset: II. Families Lycosidae, Pisauridae, Agelinidae, Mimetidae, Theridiidae, Tetragnathidae, Argiopidae. Journal of Zoology (London) 156:239–256.

Merrett, P. 1983. Spiders collected by pitfall trapping and vacuum sampling in four stands of Dorset heathland representing different growth phases of heather. Bulletin of the British Arachnological Society 6:14–22.

Merrett, P. & R. Snazell. 1983. A comparison of pitfall trapping and vacuum sampling for assessing spider faunas on heathland at Ashdown Forest, south-east England. Bulletin of the British Arachnological Society 6:1–13.

Mommertz, S., C. Schauer, N. Koesters, A. Lang & J. Filser. 1996. A comparison of D-vac suction, fenced and unfenced pitfall trap sampling of epigeal arthropods in agro-ecosystems. Annales Zoologici Fennici 33:117–124.

Morrill, W.L., D.G. Lester & A.E. Wrona. 1990. Factors affecting the efficiency of pitfall traps for beetles (Coleoptera: Carabidae and Tenebrionidae). Journal of Entomological Science 25:284–293.

Morton, S.R., M.W. Gilliam, K.R. Jones & M.R. Flemming. 1988. Relative efficiency of different pit-trap systems for sampling reptiles in spinifex grasslands. Australian Wildlife Research 15:571–577.

Muma, M.H. & K.E. Muma. 1949. Studies on a population of parry spiders. Ecology 30:173–196.

New, T.R. 1999. Untangling the web: Spiders and the challenges of invertebrate conservation. Journal of Insect Conservation 3:251–256.

Niemelä, J., E. Halme, T. Pajunen & Y. Haila. 1986. Sampling spiders and carabid beetles with pitfall traps: The effects of increased sampling effort. Annales Zoologici Fennici 52:109–111.

Niemelä, J., J. Kotze, A. Ashworth, P. Brandmayr, K. Desender, T. New, L. Penev, M. Samways & J. Spence. 2000. The search for common anthropogenic impacts on biodiversity: A global network. Journal of Insect Conservation 4:3–9.

Pimm, S.L. & P. Raven. 2000. Biodiversity: Extinction by numbers. Nature 403:843–845.

Primer E. 2001. Primer 5 for Windows. Version 5.2.2. Plymouth Marine Laboratory, Plymouth.

Purvis, A. & A. Hector. 2000. Getting the measure of biodiversity. Nature 405:212–219.

Raven, P.H. & E.O. Wilson. 1992. A fifty-year plan for biodiversity surveys. Science 258:1099–1100.

Riecken, U. 1999. Effects of short-term sampling

on ecological characterization and evaluation of epigeic spider communities and their habitats for site assessment studies. Journal of Arachnology 27:189–195.

Samu, F. & G.L. Lövei. 1995. Species richness of a spider community (Araneae): Extrapolation from simulated increasing sampling effort. European Journal of Entomology 92:633–638.

Samu, F. & M. Sárospataki. 1995. Design and use of a hand-held suction sampler, and its comparison with sweep net and pitfall trap sampling. Folia Entomologica Hungarica 56:195–203.

Skerl, K. & R. Gillespie. 1999. Spiders in conservation: Tools, targets and other topics. Journal of Insect Conservation 3:249–250.

Southwood, T.R.E. 1966. Ecological Methods with Particular Reference to the Study of Insect Populations. Methuen, London.

Spence, J.R. & J.K. Niemelä. 1994. Sampling carabid assemblages with pitfall traps: The madness and the method. Canadian Entomologist 126:881–894.

SPSS. 1996. SPSS 7.5 for Windows. SPSS Incorporated.

Standen, V. 2000. The adequacy of collecting techniques for estimating species richness of grassland invertebrates. Journal of Applied Ecology 37:884–893.

Stork, N.E. & M.J. Samways. 1995. Inventorying and monitoring biodiversity. Pp. 453–543. *In* Global Biodiversity Assessment. (V.H. Heywood, ed.). United Nations Environment Programme and Cambridge University Press, Cambridge.

Topping, C.J. & M.L. Luff. 1995. Three factors affecting the pitfall catch of linyphiid spiders (Araneae: Linyphiidae). Bulletin of the British Arachnological Society 10:35–38.

Topping, C.J. & K.D. Sunderland. 1992. Limitations to the use of pitfall traps in ecological studies exemplified by a study of spiders in a field of winter wheat. Journal of Applied Ecology 29: 485–491.

Turnbull, A.L. 1973. Ecology of the true spiders (Araneomorphae). Annual Review of Entomology 18:305–348.

Uetz, G.W. & J.D. Unzicker. 1976. Pitfall trapping in ecological studies of wandering spiders. Journal of Arachnology 3:101–111.

Underwood, A.J. 1997. Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance. Cambridge University Press, Cambridge.

Ward D.F., New T.R. & Yen A.L. 2001. Effects of pitfall trap spacing on the abundance, richness and composition of invertebrate catches. Journal of Insect Conservation. 5:47–53.

Williams, D.F. & S.E. Braun. 1983. Comparison of pitfall and conventional traps for sampling small mammal populations. Journal of Wildlife Management 47:841–845.

Wilson, E.O. 1985. The biodiversity crisis: A challenge to science. Issues in Science and Technology 2:20–29.

Work T.T., Buddle C.M., Korinus L.M. & Spence J.R. 2002. Pitfall trap size and capture of three taxa of litter-dwelling arthropods: Implications for biodiversity studies. Environmental Entomology 31:438–448.

Zar, J.H. 1984. Biostatistical Analysis. Second Edition. Prentice-Hall, Englewood Cliffs, New Jersey.

Manuscript received 13 December 2001, revised 19 February 2004.

2005. The Journal of Arachnology 33:703–710

MALE RESIDENCY AND MATING PATTERNS IN A SUBSOCIAL SPIDER

Barrett A. Klein[1,4], **Todd C. Bukowski**[2], and **Leticia Avilés**[2,3]: [1]Department of Entomology, Forbes Building, Room 410, University of Arizona, Tucson, AZ 85721 USA. E-mail: pupating@mail.utexas.edu;; [2]Department of Ecology and Evolutionary Biology, Biological Science West, University of Arizona, Tucson, Arizona 85721 USA; [3]Department of Zoology, University of British Columbia, Vancouver, BC, V6T 1Z4 Canada

ABSTRACT. Male mating strategies are often deployed with regard to female maturity and receptivity, possibly in response to sperm utilization patterns on the part of the female. We examined the pattern of male residency with females during the mating period of the subsocial spider *Anelosimus* cf. *jucundus* (Araneae, Theridiidae). We first examined patterns of male cohabitation with naturally occurring penultimate instar and adult females in the field. Males were significantly more likely to be found in association with adult females, rather than with penultimate instar females. Penultimate instar and virgin adult females of known age were then placed into the field and monitored for residency by subsequently marked males. Males were, again, significantly more likely to be found in association with adult females, rather than with penultimate-instar females, although we were unable to determine if this pattern was due to differential arrival or to differential retention of males at adult female web sites. Aspects of *A.* cf. *jucundus* natural history, including duration of male residency and frequency of mating in the field, are provided for the first time. We discuss the patterns of male residency in relation to predictions based on sperm utilization patterns by female *A.* cf. *jucundus* spiders.

Keywords: *Anelosimus*, female maturity, male cohabitation, residency, sperm utilization

Male reproductive success is largely determined by the number of mates males are able to access (Bateman 1948; Jones, et al. 2000). In spiders, where males tend to move around in search of females, a male's mating success will depend on his ability to locate females of the appropriate age and reproductive status and to assess potential paternity success once a female has been located. When females mate multiple times, sperm priority patterns should influence male reproductive strategies (Austad 1984; Eberhard et al. 1993). When paternity is biased towards the first male to mate, males should seek out and guard females who are approaching the final molt (Jackson 1980; Christenson & Goist 1979; Austad 1982; Toft 1989; Watson 1990; Dodson & Beck 1993; Eberhard et al. 1993; Bukowski & Christenson 1997; Bukowski et al. 2001; but see Masumoto 1991). In contrast, males should seek out already mature females when paternity is not biased with respect to male mating order (Eberhard et al. 1993; Schneider 1997) or when paternity is biased towards the last male to mate (Uhl 1998; West & Toft 1999). In the latter case, post-copulatory guarding of females is expected. We examined male mate-finding and residency patterns in relation to female maturity in *Anelosimus* cf. *jucundus*, a subsocial spider species in which, for reasons we discuss below, we suspected sperm utilization patterns to be unbiased with respect to male mating order.

Anelosimus cf. *jucundus*, a species to be described shortly (I. Agnarsson in press), is relatively common in riparian regions of southern Arizona. Following a period of maternal care, *A.* cf. *jucundus* siblings remain together in their natal nest until close to sexual maturation, communally capturing and feeding on prey. All clutchmates eventually disperse and establish individual webs at relatively short distances from the natal nest (5 cm–5 m, median = 46 cm; Powers & Avilés 2003). Dis-

[4] Current address: Dept. of Ecology, Evolution and Behavior, Section of Integrative Biology, Univ. of Texas at Austin, Austin, TX 78712.

persal typically occurs during the ante-penultimate and penultimate stadia (Avilés & Gelsey 1998). Following dispersal, males and females mature in their individual webs. Although both sexes mature during the same stadium (Avilés & Gelsey 1998), males do so on average nine days earlier than their sibling females (Bukowski & Avilés 2002). After maturation, females typically remain in the webs where they matured while males set out in search of females. While the sex ratio in nests prior to dispersal is even, postdispersal sex ratios are significantly female-biased (Avilés & Gelsey 1998).

The patterns of sexual receptivity in *A.* cf. *jucundus* differ for males and females. Males become sexually active within approximately two days following their final molt, while females become sexually receptive an average of ten days following their final molt (Bukowski & Avilés 2002). The probability of a male courting a female appears to increase as the female gets older (Bukowski & Avilés 2002).

Females readily remate under laboratory conditions and males do not release significantly different numbers of sperm to virgin and non-virgin females (Bukowski & Aviles, unpub. data, using methods of Bukowski et al. 2001 to quantify sperm). Given that paternity patterns in spiders largely reflect the numbers of sperm released (Christenson 1990; Bukowski & Christenson 1997; Schneider et al. 2000; Elgar et al. 2000; Bukowski et al. 2001), we predict that *A.* cf. *jucundus* will have a paternity pattern that is unbiased with respect to male mating order. In such a case, males should preferentially seek out adult rather than subadult females. Here we experimentally examine this prediction and present the first natural history data on mating frequency under field conditions in this spider species.

METHODS

We conducted our studies in Garden Canyon, a riparian area in the Huachuca Mountains of southeastern Arizona (31.51°N, 110.31°W; 1600–2000 m). *Anelosimus* cf. *jucundus* primarily inhabit juniper trees alongside permanent streams in this area (Fig. 1). Our study involved an early phase, in which we censused naturally occurring webs for patterns of male/female cohabitation, and a later, experimental phase, in which we examined male residency patterns in artificially-established subadult and adult females' webs.

Early census of naturally-occurring webs.—On 14 and 24 June 2000, we examined naturally occurring, active, post-natal dispersal webs (n = 293) for the presence of subadult and adult males and females. We identified new, active webs containing dispersed individuals by the relative lack of debris, smaller size, and presence of recently maintained capture threads. We recorded the instar (immature versus adult) and sexes of all animals in each web.

Artificially-established webs.—On 8 and 13 July 2000, we returned to their collection site 27 penultimate-instar females and 54 adult females that had been individually raised in the laboratory. These spiders had been collected as penultimate-instar females one to two weeks earlier, held individually in 125 ml or 30 ml plastic containers, and fed ad libitum on house flies (*Musca domestica*), walnut flies (*Rhagoletis juglandis*), and fruit flies (*Drosophila melanogaster*).

The spiders were returned to a large patch of naturally occurring *A.* cf. *jucundus* webs to ensure the presence of naturally occurring males. We placed individual females in open 125 ml containers, which we attached to branches of juniper trees. We covered each branch with a fine nylon mesh net to encourage web-construction at the selected site and prevent males or predators from visiting until initiation of the observation period (Fig. 2). When the nets were removed 48 hours later, females had usually expanded their webs from the containers to the surrounding vegetation.

Web sites (defined here as the area within approximately ten centimeters of the female's web) were censused every 1–2 hours over a 24 hour period, every other day. Females returned to the field on 8 July were censused over a period of seven days, and females returned to the field on 13 July were censused over a period of three days. During each census, females were recorded as present or absent and the occurrence of mating and male-male physical contact was monitored.

We individually marked all males that appeared at a female's web site (n = 76) with water–based acrylic paints so that we could determine their duration of residency, occurrences of mating and relocation distances.

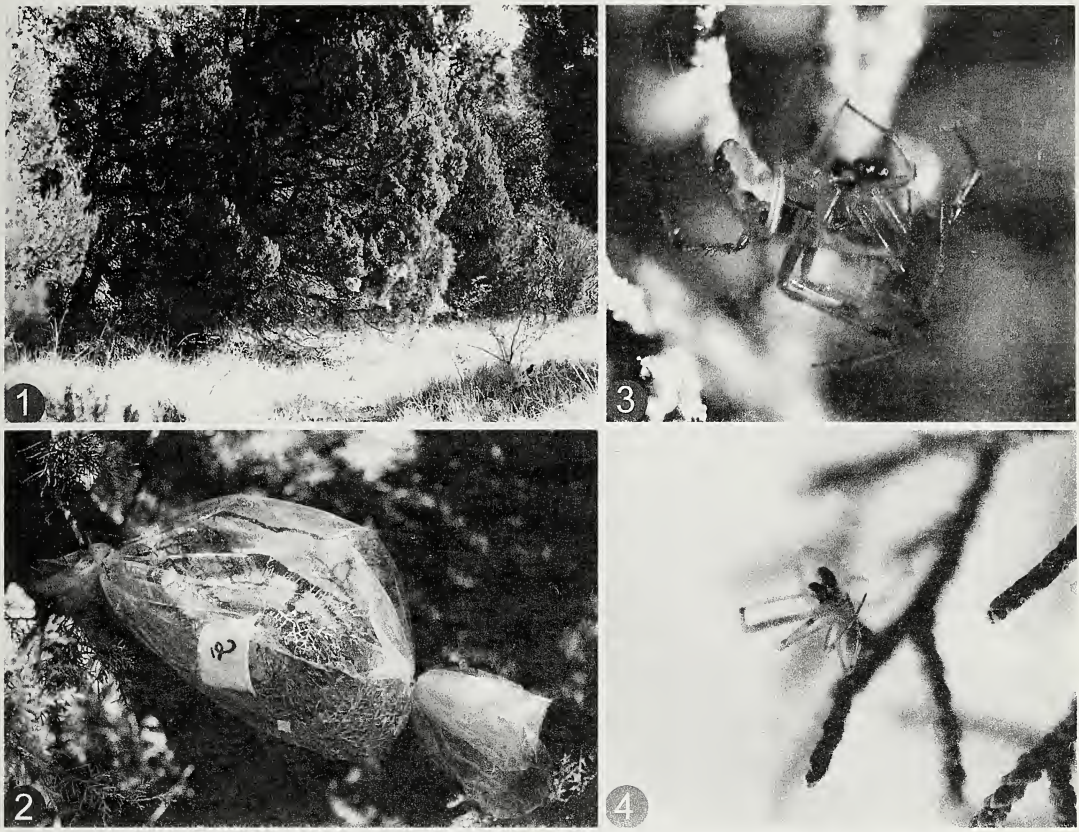


Figure 1.—Juniper trees in the Huachuca Mountains of Arizona, where we artificially established webs of female *A.* cf. *jucundus* spiders in a community of naturally-occurring conspecifics.

Figure 2.—Artificially-established female web site, temporarily surrounded by netting to deter predation or escape as she expanded her web beyond the cup (labeled "2" and attached to a juniper branch).

Figure 3.—Copulation (male on left, female on right).

Figure 4.—Following an extended bout of male-male aggression, this male had tumbled below its combatant, who proceeded to court and mate with the resident female.

First, each unmarked male was removed from a female's web site immediately upon detection or following copulation. Each male was uniquely marked by gently guiding him into a piece of mesh netting and dabbing acrylic paint onto his opisthosoma. Following marking, the male was returned to his place of removal. Most males remained without obvious behavioral long term effects, although six (of 82) males were dropped and lost, and two males were being consumed by female residents during the census following each male's marking.

Matings were defined as pairs in copula with at least one male pedipalp inserted in the female. *Anelosimus* cf. *jucundus* males typically have one insertion with each palp during mating. Matings typically last approximately 135 minutes per pedipalp, with an interim of 35 minutes between pedipalps (Bukowski & Avilés unpub. data). Matings, in light of their lengthy durations, were unlikely to have been undetected during a day of censusing with 1–2 hour inter-census periods.

Statistical analyses.—For all maturity analyses, each female was classified as penultimate instar or adult. If seen at a web site during consecutive census periods, a spider was assumed to have remained for the duration between observations. If observed only during a single census period, a spider was considered to have remained for one hour (for duration study purposes). Each adult female web site (n = 54) was checked an average of

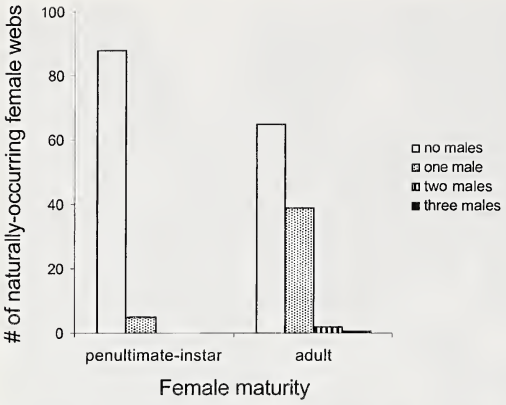


Figure 5.—Male residency in relation to female maturity in naturally-occurring webs. Number of males residing in each web (zero, one, two, or three males) is plotted against the number of naturally-occurring female webs with respect to female maturity. These data are the result of an early field survey.

30 times and each penultimate-instar female web site (n = 27) was checked an average of 27 times. The proportion of observations that a female's web site was visited by a male and the number of different males involved was recorded for each female. Each female then served as a single observational unit for the purpose of analyses. All analyses used data from the entire study period, except for the duration of male-female encounters and mating analyses, which used data collected after the first day (when male marking began). Except where noted, only data concerning present and live spiders were analyzed.

Data from the two sets of animals (those placed into the field on 8 and 13 July) were combined when they exhibited no significant differences. Percentage data were arcsine square root transformed prior to analysis. Duration data, which were non-normally distributed, were analyzed using nonparametric tests. Summary statistics of continuous variables are reported as $\bar{X}$ ± standard error (SE). Alpha was set at 0.05 for all tests and all tests are two-tailed. Data were analyzed with the JMP IN (version 4.0.3; SAS Institute Inc. 2001) computer package, or, in the case of rates of male arrival, with Systat (Systat Software, Inc.).

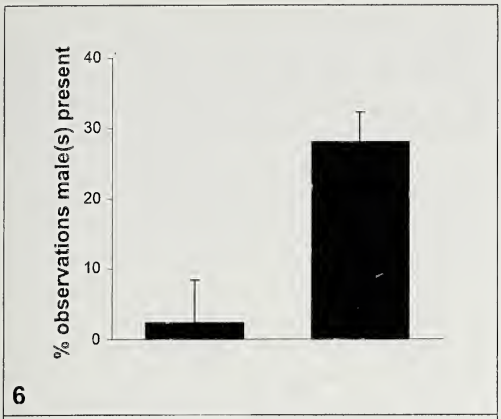
RESULTS

Male residency in relation to female maturity: naturally-occurring webs.—Male cohabitation with immature females was rarely observed in naturally-occurring *A.* cf. *jucundus* webs during our early census. The webs of adult females were far more likely to contain an adult male (42 of 107 females, 39.3%) than were the webs of penultimate-instar females (5 of 93 females, 5.4%; χ^2 = 35.79, P < 0.0001). Of those webs that contained males, most adult females (n = 39) and all five penultimate-instar females each contained a single male. Two of the adult females each cohabited with two males, and the web of one adult female contained three male visitors (Fig. 5). Since we were interested in male residency with females and female-female residency was rare, four webs that each contained two adult females and two webs that each contained two penultimate-instar females were excluded from the previous analysis.

All penultimate-instar males were found as solitary individuals (n = 48). In contrast, at least as many adult males were found with a female (n = 46) as without (n = 38). In one additional case, three adult males were found together in one web without a female.

Male residency in relation to female maturity: artificially-established webs.—Of the females placed into the field, many (47 of 81, 58.0%) disappeared from their web sites before the study ended. The web sites of adult females were, again, far more likely to contain an adult male than were the web sites of penultimate-instar females (27.9 ± 4.3% versus 2.4 ± 6.1% of the observations per female; n = 36 and 18 females, respectively; t_{52} = 3.41, P = 0.0013; Fig. 6). Adult females also had a greater number of male cohabitants per hour (0.37 ± 0.06) than did penultimate-instar females (0.03 ± 0.08; t_{52} = 3.28, P = 0.0019; n = 36 and 18 females, respectively; Fig. 7). All but five (of 54) male visitations were by new, unmarked males. The five exceptions included one male who returned to the same female after a 37 hour absence, two males who each traveled to a second female, and one male who traveled to three different females.

Although males appeared to arrive to adult female web sites at twice the rate than to subadult female web sites (to 33 out of 118 available adult females, or 28%, versus 6 out of 43 available subadult females, or 14%), this difference was not statistically significant with our sample size (Mantel-Haenzel χ^2 = 2.37, P = 0.12, for the comparison of numbers of new



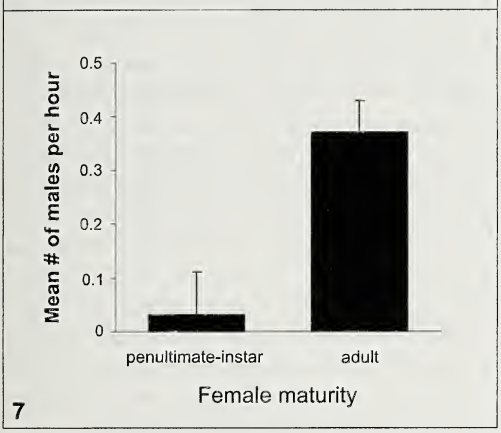


Figure 6.—Male residency in relation to female maturity in artificially-established webs: percent of field observations in which at least one male was present (± SE).

Figure 7.—Male residency in relation to female maturity in artificially-established webs: mean number of male residents per hour (± SE).

males arriving per total females available at each of 18 different census periods). Males also tended to stay longer at adult female web sites (see next section), but this effect appeared to reflect whether copulation occurred or not, rather than female age per se.

Duration of male residency.—Because of the periods between census days during which the nests were not monitored, we can only provide estimates of the minimum and maximum possible male residence times. In cases where male residence periods had either already been initiated when observations had started or had not yet concluded when observations ended, we have taken the period actually observed as the minimum male residence time. This period plus the unobserved period either before or after the start of a census day, as appropriate to the case, gives us a maximum possible residence time. Given these considerations, the median male residence time we observed was bracketed between a minimum of five and a maximum of 11 hours.

Based on our minimun male residence estimates (period actually observed), males spent more time per visit with adult females with whom they mated than with any other females (median = 18.5 hours, versus 5 hours for adults not observed to mate, and 3 hours for penultimate-instar females; n = 10, 37, and 6 visits, respectively; χ^2 = 12.1, 2 df, P = 0.002; Fig. 8). Post-copulatory periods ranged from three to 33 hours (n = 10), with seven cases lasting seven hours or less. If three cases in which the period had not yet concluded when observations ended are included, a floor for the median post-copulatory period is estimated at six hours.

In a few instances, more than one male could be observed at a female's web site (Table 1). Cohabiting males engaged in agonistic interactions, including foreleg tapping and locking of chelicerae and legs (n = three pairs of males in the presence of three different females). One battle sent a male tumbling and appearing temporarily dead (Fig. 4), while his combatant copulated with the resident female (Fig. 3). Male–induced *coitus interruptus,* resulting in no resumption of copulation, was also observed in one case where two males were simultaneously present with a female.

Mating frequency.—Nineteen of the 36 adult females (52.7%) were observed mating with at least one male over the study period. Eleven of these females (57.9%) were each observed mating with a single male. The remaining eight of these females (42.1%) were each observed mating with two males. The average number of males a female copulated with over the active observation period (an average of 38.8 observation-hours per female) was therefore 0.75, which corresponds to 0.47 males per female per day, if we assume a similar mating rate during non-observed periods, or, more conservatively, 0.22 males per female per day if we assume that all matings were observed during the recorded period of each female.

Some marked males (10 of 76, 13.2%) were observed at the web sites of two (n = 9) or

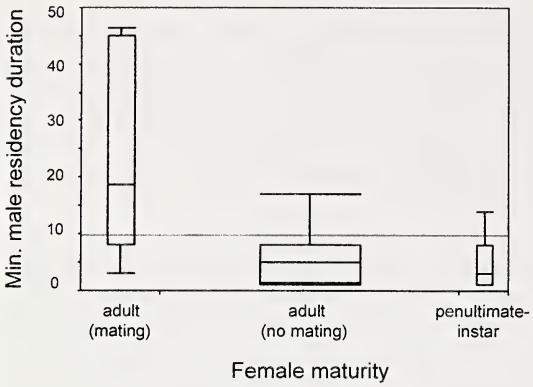


Figure 8.—Estimates of the range (outermost lines in each graph), 25th and 75th quantiles (edge of boxes), and medians (lines inside the boxes) of the minimum duration of male residency (based on period actually observed) with respect to female age and mating status. Males spent more time per visit with adult females with whom they mated (median = 18.5 hours; n = 10 visits), than with adults with whom they were not observed to mate (median = 5 hours; n = 37 visits), or with penultimate-instar females (median = 3 hours; n = 6 visits).

three (n = 1) females. However, because males could not be tracked as reliably as females (and several of the females were absent or dead at the time of male visitation), only one of these males was actually observed to mate more than once. Overall, ten of 48 (20.8%) visits by marked males to adult female web sites were observed to result in copulation (Fig. 8).

Measurements of distances between female web sites that males successively visited showed an average travel distance of 2.0 ± 0.4 m (range: < 1–4 m, n = 11 males) over an average of 21.5 ± 4.5 hours (range: 11.5–51.0 hours, n = 11). Three of the males each traveled four meters in an average 32.3 ± 11.4 hours.

DISCUSSION

Anelosimus cf. *jucundus* males were much more likely to be found on the webs of adult females than on those of penultimate-instar females, both in a survey of free-ranging spiders and when females of known age and reproductive history were placed into the field. Adult females also had a greater number of male residents per hour than did penultimate-instar females.

The mechanism responsible for these divergent residency patterns remains unclear. Males could preferentially arrive at the webs of adult females or arrive equally at both adult and juvenile female webs, but be preferentially retained by adult females. Our data show a nonsignificant trend towards differential arrival at adult webs and significant retention when copulation occurs. Although a greater sample size will be needed to definitely address this issue, the trend towards preferential arrival at adult female web sites suggests that females may be producing a distance-acting signal or cue guiding males to their webs. Distance-acting pheromones released by females have been demonstrated to attract males in both *Pardosa milvina* wolf spiders (Searcy et al. 1999) and in *Agelenopsis aperta* desert spiders (Papke et al. 2001). If males arrive at the webs of adult and juveniles equally, then some process associated with interaction with the female must influence duration of male residency.

Nearly half of the females observed mating copulated with more than one male, suggesting that multiple mating by females is common in this species. Matings were not predictably followed by continued male residence at the females' web sites (in 60% of the cases the male departed in six hours or less), so prolonged post-copulatory guarding appears to be absent in these spiders. Male residency subsequent to copulation could simply involve time spent by males inducting sperm into their pedipalps for subsequent matings or their facultative use of females' webs for food and shelter, rather than a means of exploiting the resident females' reproductive biology. Given that males differentially reside with adult females, females multiply mate, and males do not exhibit post-copulatory guarding, male mating order may not be an important determinant of paternity in *A.* cf. *jucundus*.

At times, more than one male entered the same adult female site. This could result in multiple matings by females with different resident males, or male-male aggressive interactions, as described earlier. Because of the scarcity of extended multiple male residencies, aggressive interactions may drive some males to search for different, unattended females.

Many adult females were observed mating during the relatively short study period. Of

Table 1.—Number and proportion of census observations with zero, one, two, or three males cohabiting with adult females in their artificially-established webs. Multiple male residency at a given female's web was uncommon. Calculations are pooled across females.

# males	# observations	% observations
0	355	57.1
1	211	33.9
2	53	8.5
3	3	0.5
Total	622	100

those females, about half were observed to mate with at least two males. Given that females become sexually receptive an average of ten days after the final molt and cease sexual receptivity after oviposition (Bukowski & Avilés 2002), a total of 20 days spans the average period of sexual receptivity for females in this species. Assuming that a female's propensity to mate does not alter dramatically over the course of these 20 days and that all matings are considered to have been observed throughout the period of censusing, a female may be calculated to mate with an average of 4.4 males during her lifetime (0.22 males per female per day × 20 days). This figure may underestimate the number of potential matings if we assume that additional matings occurred during the unobserved periods. Alternatively, this figure may overestimate the number of potential matings if female receptivity or the frequency of male visitation to females' web sites diminished as the 20-day female active period progressed, although we have no evidence negating or supporting either a diminished female receptivity or reduced male visitation over time. All matings within census days were likely to have been observed and recorded because times between censuses were shorter than the average copulation duration. Matings occurring during the much longer period between census days, on the other hand, could have been missed.

The male residency and female mating patterns exhibited by *A.* cf. *jucundus* have important implications for the pattern of sperm utilization at fertilization. When the fertilization pattern is biased towards first males, males differentially cohabit with juvenile females approaching the final molt when the females first become sexually receptive (Austad 1982; Christenson & Cohn 1988; Watson 1990; Bukowski & Christenson 1997; Bukowski et al. 2001). When the fertilization pattern is biased towards last males, males should preferentially seek out and guard adult females (Uhl 1998; West & Toft 1999). When the sperm of two or more males mix equally within the female, males should seek out adult females regardless of female age (Eberhard et al. 1993). Our data suggest that *A.* cf. *jucundus* exhibit either last male precedence or sperm mixing. Other data on sperm release patterns in this species, along with no evidence of mate guarding, provide support for sperm mixing, since the first and second males to mate with a female were found to transfer equal numbers of sperm (Bukowski & Avilés, unpub. data). Several studies have shown that when two males mating with a female transfer equal numbers of sperm, the two males typically sire equal numbers of offspring (Bukowski & Christenson 1997; Schneider et al. 2000; Elgar et al. 2000). If a male were to reside with a penultimate instar female until she became sexually receptive, he would likely visit and mate with fewer females, siring fewer offspring than a male that exclusively visits adult females.

Understanding the role of female maturity, mating receptivity and subsequent sperm utilization is contingent upon learning more about the natural history of *A.* cf. *jucundus* spiders. Precisely determining male arrival rates and residency durations relative to female maturity could serve as the next step in understanding the mechanisms driving their sexual interactions.

ACKNOWLEDGMENTS

We thank Sheridan Stone and the Wildlife Management Office for access to the spiders of Garden Canyon, and Natalie Doerr and Terry A. Bukowski for helping with field data collection. Asher Cutter, Greta Binford, Jeff Smith, Eileen Hebets, Kim Powers, two anonymous reviewers and the editors offered fruitful comments on drafts of this paper. Voucher specimens of both sexes reside within the National Museum of Natural History Spider Collection, Washington D.C., USA. This research was supported by NSF grant DEB-9815938 to Leticia Avilés.

LITERATURE CITED

Agnarsson, I. In press. A revision of the New World *eximius* lineage of *Anelosimus* (Araneae, Theridiidae) and a phylogentic analysis using worldwide exemplars. Zoological Journal of the Linnean Society.

Austad, S.N. 1982. First male sperm priority in the bowl and doily spider *Frontinella pyramitela* (Walckenaer). Evolution 36:777–785.

Austad, S.N. 1984. A classification of alternative reproductive behaviors and methods for field-testing ESS models. American Zoologist 24: 309–319.

Avilés, L. & G. Gelsey. 1998. Natal dispersal and demography of a subsocial *Anelosimus* species and its implications for the evolution of sociality in spiders. Canadian Journal of Zoology 76: 2137–2147.

Bateman, A.J. 1948. Intra-sexual selection in *Drosophila*. Heredity 2:349–368.

Bukowski, T.C. & L. Avilés. 2002. Asynchronous maturation of the sexes may limit close inbreeding in a subsocial spider. Canadian Journal of Zoology 80:193–198.

Bukowski, T.C. & T.E. Christenson. 1997. Determinants of sperm release and storage in a spiny orbweaving spider. Animal Behaviour 53:381–395.

Bukowski, T.C., C.D. Linn & T.E. Christenson. 2001. Copulation and sperm release in *Gasteracantha cancriformis* (Araneae: Araneidae): differential male behaviour based on female mating history. Animal Behaviour 62:887–895.

Christenson, T.E. 1990. Natural selection and reproduction: a study of the golden orb- weaving spider, *Nephila clavipes*. Pp. 149–74. *In* Contemporary Issues in Comparative Psychology. Edited by D.A. Dewsbury. Sinauer, Sunderland, MA.

Christenson, T.E. & J. Cohn. 1988. Male advantage for egg fertilization in the golden orb-weaving spider (*Nephila clavipes*). Journal of Comparative Psychology 102:312–18.

Christenson, T.E. & K.C. Goist. 1979. Costs and benefits of male-male competition in the orb-weaving spider *Nephila clavipes*. Behavioral Ecology and Sociobiology 5:87–92.

Dodson, G.N. & M.W. Beck. 1993. Pre-copulatory guarding of penultimate females by male crab spiders, *Misumenoides formosipes*. Animal Behaviour 46:951–959.

Eberhard, W.G., S. Guzman-Gomez & K. Catley. 1993. Correlation between spermathecal morphology and mating systems in spiders. Biological Journal of the Linnean Society 50:197–209.

Elgar, M.A., J.M. Schneider & M.E. Herberstein. 2000. Female control of paternity in the sexually cannibalistic spider *Argiope keyserlingi*. Proceedings of the Royal Society of London, Series B-Biological Sciences 267:2439–2443.

Jackson, R.R. 1980. The mating strategy of *Phidippus johnsoni* (Araneae, Salticidae): II, Sperm competition and the function of copulation. Journal of Arachnology 8:217–240.

Jones, A.G., G. Rosenqvist, A. Berglund, S.J. Arnold, and J.C. Avise. 2000. The Bateman gradient and the cause of sexual selection in a sex-role reversed pipefish. Proceedings of the Royal Society of London Series B-Biological Sciences 267:677–680.

Masumoto, T. 1991. Males' visits to females' webs and female mating receptivity in the spider, *Agelena limbata* (Araneae, Agelenidae). Journal of Ethology 9:1–7.

Papke, M.D., S.E. Riechert, & S. Schulz. 2001. An airborne female pheromone associated with male attraction and courtship in a desert spider. Animal Behaviour 61:877–886.

Powers, K.S. and L. Avilés. 2003. Natal dispersal patterns of a subsocial spider *Anelosimus* cf. *jucundus* (Theridiidae). Ethology 109:1–13.

Schneider, J.M. 1997. Timing of maturation and the mating system of the spider, *Stegodyphus lineatus* (Eresidae): how important is body size? Biological Journal of the Linnean Society 60:517–525.

Schneider, J.M., M.E. Herberstein, F.C. De Crespigny, S. Ramamurthy, & M. Elgar. 2000. Sperm competition and small size advantage for males of the golden orb-web spider *Nephila edulis*. Journal of Evolutionary Biology 13:939–946.

Searcy, L.E., A.L. Rypstra, & M.H. Persons. 1999. Airborne chemical communication in the wolf spider *Pardosa milvina*. Journal of Chemical Ecology 25:2527–2533.

Toft, S. 1989. Mate guarding in two *Linyphia* species (Araneae: Linyphiidae). Bulletin of the British Arachnological Society 8:33–37.

Uhl, G. 1998. Mating behaviour in the cellar spider, *Pholcus phalangioides*, indicates sperm mixing. Animal Behaviour 56:1155–1159.

Watson, P.J. 1990. Female-enhanced male competition determines the first mate and principle sire in the spider *Linyphia litigiosa* (Linyphiidae). Behavioral Ecology and Sociobiology 26:77–90.

West, H.P. & S. Toft. 1999. Last-male sperm priority and the mating system of the haplogyne spider *Tetragnatha extensa* (Araneae: Tetragnathidae). Journal of Insect Behavior 12:433–450.

Manuscript received 7 October 2003, revised 30 June 2004.

2005. The Journal of Arachnology 33:711–714

A REDESCRIPTION OF *CHRYSSO NIGRICEPS* (ARANEAE, THERIDIIDAE) WITH EVIDENCE FOR MATERNAL CARE

Jeremy Miller[1,3] and **Ingi Agnarsson**[1,2,4]: [1]Department of Entomology, National Museum of Natural History, NHB-105, Smithsonian Institution, PO Box 37012, Washington, DC 20013-7012, U.S.A.; [2]Department of Biological Sciences, George Washington University, 2023 G Street NW, Washington, D.C. 20052, USA

ABSTRACT. *Chrysso nigriceps* is redescribed and the male is described for the first time based on material from Colombia. Evidence for maternal care of juveniles in *Chrysso* is presented. This evidence is consistent with predictions based on phylogenetic analysis that maternal care is primitively present in the lost colulus clade, the lineage containing all social theridiids.

Keywords: *Chrysso*, evolution of sociality, maternal care, taxonomy, South America

Chrysso nigriceps (Keyserling 1884) was described based on a female specimen from Colombia. In a revision of *Chrysso* O. Pickard-Cambridge 1882 from the Americas, Levi (1957) redescribed the female, but to date the male remains unknown. Here we redescribe *C. nigriceps* and provide a description of the male. We observed juveniles of *C. nigriceps* cohabitating in the female web (Fig. 1), suggesting some degree of maternal care. Kuntner (pers. comm.) also observed juveniles in adult webs of an Indonesian species, *Chrysso* nr. *argyrodiformis* (Yaginuma 1952). To our knowledge, these observations represent the first evidence of maternal care of juveniles reported in *Chrysso*. Although preliminary, our evidence for maternal care in *Chrysso* is consistent with Agnarsson's (2004) phylogenetic conclusion that maternal care is primitively present in the subfamily Theridiinae.

A growing body of evidence supports the "maternal care route" hypothesis to web sharing sociality (Avilés 1997; Agnarsson 2002, 2004). It states that social behavior evolved via temporal extension of maternal care (see Kullmann 1972; Avilés 1997 for reviews). Tolerance among juveniles is maintained over an increasing period of their life-span, culminating in permanent web sharing sociality (quasisociality) with extensive cooperation among adults. The optimization of maternal care (or simply the brief coexistence of mother and young in the web) on a phylogenetic tree is therefore an important step in reconstructing the evolutionary path from solitary to social lifestyle.

Agnarsson (2002, 2004) discussed the progression from solitary lifestyle to quasisociality in a phylogenetic context. In his phylogeny, maternal care optimized to the node leading to all instances of sociality (*Anelosimus* Simon 1891 plus Theridiinae, or the "lost colulus clade", see Agnarsson 2004, fig. 106). Based on this, he predicted that maternal care should be widespread within the lost colulus clade, a lineage containing hundreds of species. However, Agnarsson (2004) pointed out that the lack of behavioral data on many key taxa in the analysis limited the power of this argument. He noted that the lack of evidence for maternal care in many of these species is due to a poverty of studies on lost colulus clade species that might have discovered maternal care in the field, rather than failed attempts to document maternal care. Agnarsson's (2004) phylogeny of theridiid genera places *Chrysso* (based on an undescribed species called *Chrysso* nr. *nigriceps*) in a key phylogenetic position, sister to the remaining theridiines. *Chrysso* was scored as unknown for maternal care, as were several other basal theridiines. Evidence for maternal care in *Chrysso* corroborates the hypothesis that maternal care is primitively present in the lost colulus clade, and that maternal care precedes sociality in evolutionary time. Note that a mo-

[3] Current address: Department of Entomology, California Academy of Science, 875 Howard Street, San Francisco, CA 94103, USA.
E-mail: jmiller@Calacademy.org
[4] Current address: Department of Botany and Zoology, The University of British Columbia, 3529-6270 University Blvd., Vancouver, BC. V6T 1Z4, Canada.

lecular phylogeny of theridiids places *Chrysso* nr. *nigriceps* in a clade with *Helvibis* Keyserling 1884 and *Theridula* Emerton 1882, together sister to the remaining theridiines (Arnedo et al. 2004). Maternal behavior remains to be documented for *Helvibis* and *Theridula* and this alternative placement of *Chrysso* does not alter the significance of our finding.

METHODS

Illustrations were modified from digital photographs taken using a Nikon DXM 1200 digital camera mounted on a Leica MZ16 A dissecting microscope. All measurements are in millimeters and were taken using a reticle in a LEICA MZ APO dissecting microscope. For further details on methods see Miller (in press) and Agnarsson (2004). Material used in this study was borrowed from the following institutions: The Natural History Museum, London (BMNH), Museum of Comparative Zoology, Harvard (MCZ), and National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

TAXONOMY

Family Theridiidae Sundevall 1833
Genus *Chrysso* O. Pickard-Cambridge 1882
Chrysso nigriceps Keyserling 1884
Figs. 1–6

Chrysso nigriceps Keyserling 1884: 154, pl. 7, fig. 95 [♀]; Levi 1957: 65, figs. 16, 32, 33 [♀]; Platnick 2004. Holotype female from Bogotá, Colombia, in BMNH, examined.

Theridion keyserlingi Petrunkevitch 1911: 198 (unjustified replacement name for *C. nigriceps*; see Levi 1957; Platnick 2004); Mello-Leitão 1941: 250; Roewer 1942: 494.

Type material.—Holotype female: COLOMBIA: *Cundinamarca*: Bogotá, Keyserling (BMNH, BM1890.7.1.8150).

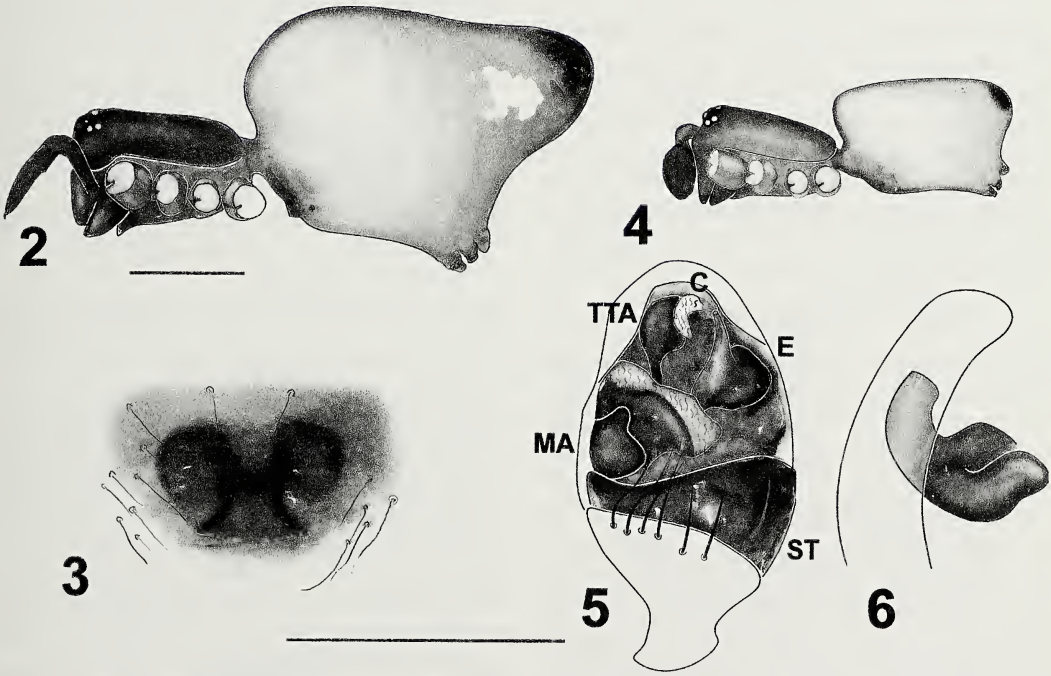
Other material examined.—COLOMBIA: *Cundinamarca*: Silvania, Res. Agua Bonita (off Carretera Sibate—Fusagasugá; 15 km from Sibate), 4°26′N, 74°20′W, 2440–2560 m, 1 February 1998, G. Hormiga (USNM), 1 ♀; same data, J. Miller (USNM), 1 ♀; La Calera, Cerro del Chocolatero, ca. 5 km NE of Bogotá, 4°42′N, 73°58′W, 3000–3145 m, 31 January 1998, G. Hormiga, J. Miller, J. Barriga, J.C. Bello, A. Sabagal (USNM), 1♀; *Valle del Cauca*: Yotoco, 1600 m, December 1976, W. Eberhard (MCZ, det. B. Opell), 2 ♂, 1 ♀, 1 juvenile ♂; Saladito above Cali, 1800 m, 3 January 1977, fog forest, H. Levi (MCZ, 57413), 1 ♀; arriba de Saladito, 1800 m (MCZ, 57412), 5 ♀, 3 egg cases; Saladito, 1800 m, 20 March 1970 (MCZ, 57417, det. Levi), 1 ♀; Saladito, 1800 m [no date] (MCZ, 57411), 1 ♀, eggs and embryonic juveniles; near Saladito, 12 October [no year] (MCZ, 57418), 4 ♀, eggs and embryonic juveniles; Cali [no date] (MCZ, 57414), 1 ♂; near Pance, P.N.N. Farallones de Cali, Res. Nat. Hato Viejo, 3°20′53″N, 76°40′07″W, 2300 m, 12 February 1998, G. Hormiga (USNM), 1 ♂; *Putumayo*: Cauda-Putumayo, road between Mocoa and Silbundoy, ca. 71,500 m [*sic*], August 1973, W. Eberhard (MCZ, 57416, det. Levi), 1 ♀.

Additional records.—ECUADOR: Bañor, Runtun Trail, 2000 m, 26 November 1939, F. M. Brown, 1 ♀ (see Levi 1957).

Diagnosis.—*Chrysso nigriceps* differs from most American *Chrysso* by the coloration of the abdomen, bright orange (light gray in alcohol) with black posterior lobe (Figs. 1, 2 & 4). Females further differ by the presence of a trapezoidal plate on the posterior margin of the epigynum (Fig. 3). Males can be diagnosed by the shape of the median apophysis in prolateral view (Fig. 6).

Description.—*Female (from Agua Bonita, Cundinamarca, Colombia):* Total length 4.40, carapace length 1.55, carapace width 1.29, sternum length 0.88, sternum width 0.87. Carapace dusky orange, darker around eyes. Sternum orange. Chelicerae orange with two promarginal teeth. Palpi dusky orange; palpal tibia with one prolateral, one retrolateral trichobothrium. Coxae, trochanters, and basal half of femora orange; distal half of femora and distal leg segments dusky orange. Leg I: femur 2.71, patella 0.58, tibia 1.85, metatarsus 2.02, tarsus 0.95, total 8.12; leg II: femur 1.87, patella 0.50, tibia 1.09 metatarsus 1.20, tarsus 0.73, total 5.40; leg III: femur 1.28, patella 0.42, tibia 0.70, metatarsus 0.78, tarsus 0.58, total 3.76; leg IV: femur 2.22, patella 0.51, tibia 1.40, metatarsus 1.33, tarsus 0.69, total 6.14. Leg formula: 1-4-2-3. Abdomen extends posteriorly beyond spinnerets, bright orange (light gray in alcohol) with black posterior tip and two white guanine patches, posterior patch larger than anterior (Figs. 1, 2). Colulus absent. Area between booklungs covered with smooth orange sternite continuous with epigynum; spermathecae separated by less than their width; epigynum with median trapezoidal plate at posterior margin (Fig. 3).

Figure 1.—*Chrysso nigriceps*. Juvenile spiders in web with adult female, Agua Bonita, Colombia.



Figures 2–6.—*Chrysso nigriceps*. 2, 3. female; 4–6. male. 2, 4. habitus, lateral view; 3. epigynum; 5. male palp, ventral view; 6. median apophysis, prolateral view. C, conductor, E, embolus, MA, median apophysis, ST, subtegulum, TTA, theridiid tegular apophysis. Upper scale bar for Figs. 2 & 4, 1 mm; lower scale bar for other figures, 0.5 mm.

Male (from Hato Viejo, Valle del Cauca, Colombia): Total length 2.77, carapace length 1.21, carapace width 1.06, sternum length 0.73, sternum width 0.70. Carapace orange. Sternum orange. Chelicerae orange with two promarginal teeth. Palpi dusky orange. Coxae, trochanters, and basal half of femora orange; distal half of femora and distal leg segments dusky orange. Leg I: femur 2.43, patella 0.49, tibia 1.76, metatarsus 1.83, tarsus 0.91, total 7.41; leg II: femur 1.65, patella 0.37, tibia 1.02, metatarsus 1.09, tarsus 0.66, total 4.78; leg III: femur 1.18, patella 0.33, tibia 0.69, metatarsus 0.73, tarsus 0.51, total 3.43; leg IV: femur 1.97, patella 0.41, tibia 1.28, metatarsus 1.24, tarsus 0.66, total 5.56. Leg formula: 1-4-2-3. Abdomen extends posteriorly slightly beyond spinnerets, light gray (in alcohol) with black posterior tip; guanine patches absent (Fig. 4). Colulus absent. Area between booklungs covered with smooth orange sternite. Palp as in Fig. 5; median apophysis diagnostic (Fig. 6).

Distribution.—Colombia and Ecuador.

Remarks.—During an expedition to Colombia, *Chrysso nigriceps* was collected from two regions, the male from near Cali, females near Bogotá. An undescribed *Chrysso* species was also collected on this same expedition. Both males and females of this undescribed species were collected from the S.F.F. Iguaqué, Boyocá, Colombia. The undescribed species was included as the exemplar representing *Chrysso* in recent phylogenetic analyses of theridiid genera, where it was referred to as *Chrysso* nr. *nigriceps* (Agnarsson 2004; Arnedo et al. 2004).

ACKNOWLEDGMENTS

Mark Harvey, Barbara Knoflach, Matjaž Kuntner, and an anonymous reviewer, provided comments that helped improve the manuscript. Thanks to Janet Beccaloni (BMNH), Jonathan Coddington and Dana De Roche (USNM), and Gonzalo Giribet and Laura Leibensperger (MCZ) for the loan of specimens. Matjaž Kuntner generously shared unpublished data on *Chrysso* in Indonesia. Colombian field assistance provided by Jonathan Coddington, Gustavo Hormiga, Eduardo Florez, Valeria Rodríguez, Darío Correa, Javier Barriga, Juan Carlos Bello, Fernando Fernández, Claudia Medina, A. Sabógal, and the Instituto von Humboldt, Instituto de Ciencias Naturales. Institutional support was provided by the National Museum of Natural History (Smithsonian Institution) and the George Washington University. This work was supported in part by an NSF-PEET (9712353) grant to Hormiga and Coddington and the USIA Fulbright program. Special thanks to Cynthia Zujko.

LITERATURE CITED

Agnarsson, I. 2002. On the relation of sociality and kleptoparasitism in theridiid spiders (Theridiidae, Araneae). Journal of Arachnology 30:181–188.

Agnarsson, I. 2004. Morphological phylogeny of cobweb spiders and their relatives (Araneae, Araneoidea, Theridiidae). Zoological Journal of the Linnean Society 141:447–626.

Arnedo, M.A., J. Coddington, I. Agnarsson, & R.G. Gillespie. 2004. From a comb to a tree: Phylogenetic relationships of the comb-footed spiders (Araneae, Theridiidae) inferred from nuclear and mitochondrial genes. Molecular Phylogenetics and Evolution. 31:225–245.

Avilés, L. 1997. Causes and consequences of cooperation and permanent-sociality in spiders. Pp. 476–498. *In* The Evolution of Social Insects and Arachnids. (J.C. Choe & B.J. Crespi, eds.) Cambridge University Press, Cambridge.

Keyserling, E. 1884. Die Spinnen Amerikas. II. Theridiidae. Nürnberg 1, 222 pp.

Kullmann, E. 1972. Evolution of social behavior in spiders (Araneae; Eresidae and Theridiidae). American Zoologist 12:419–426.

Levi, H.W. 1957. The spider genera *Chrysso* and *Tidarren* in America (Araneae: Theridiidae). Journal of the New York Entomological Society 63:59–81. [Date on volume 1955; actually published in 1957.]

Mello-Leitão, C.F. de. 1941. Catalogo das aranhas da Colombia. Anais Academia brasileira de Ciencias 13:233–300.

Miller, J.A. In press. Review of erigonine spider genera in the Neotropics (Araneae: Linyphiidae, Erigoninae). Zoological Journal of the Linnean Society.

Petrunkevitch A. 1911. A synonymic index-catalogue of spiders of North, Central and South America with all adjacent islands, Greenland, Bermuda, West Indies, Terra del Fuego, Galapagos, etc. Bulletin of the American Museum of Natural History 29:1–791.

Platnick, N.I. 2004. The world spider catalog, version 4.5. American Museum of Natural History, online at http://research.amnh.org/entomology/spiders/catalog/index.html

Roewer, C. F. 1942. Katalog der Araneae von 1758 bis 1940. Bremen, 1:1–1040.

Manuscript received 5 February 2004, revised 12 May 2004.

2005. The Journal of Arachnology 33:715–718

A 'SWIMMING' *HETEROPODA* SPECIES FROM BORNEO (ARANEAE, SPARASSIDAE, HETEROPODINAE)

Peter Jäger: Forschungsinstitut und Naturmuseum Senckenberg, Senckenberganlage 25, D-60325 Frankfurt am Main, Germany. E-mail: Peter.Jaeger@Senckenberg.de

ABSTRACT. *Heteropoda natans* new species (Araneae, Sparassidae, Heteropodinae) is described from Borneo. Additional illustrations of the genitalia of *H. hosei* (Pocock 1897) are provided for comparison purposes. The lectotype of *H. hosei* is designated.

Keywords: Sparassidae, *Heteropoda*, taxonomy, new species, Borneo

The sparassid subfamily Heteropodinae includes eight genera, of which *Heteropoda* Latreille 1804 is by far the most diverse with about 190 nominal species (Jäger 2002). The genus has not been revised in recent times except for the species from the Australian region (Davies 1994).

In 1998 Satie Airamé and Petra Sierwald observed and collected specimens of an unidentified *Heteropoda* species in a lowland rainforest on Borneo (Malaysia, Sabah). Individuals were observed in a laboratory and the hunting behavior was investigated. Hunting on the water surface could be shown the first time for the family Sparassidae. Even though the observations were made under artificial conditions, there is evidence that this behavior also occurs in natural situations (Airamé & Sierwald 2000).

Two *Heteropoda* species have been described previously from Borneo: *H. hosei* Pocock 1897 and *H. obtusa* Thorell 1890. After comparing the new material with type material and original descriptions, it appeared to be a species new to science, which is described below. Conspecifity of *H. obtusa* with the here described new species can be excluded by the distinctly smaller size of *H. obtusa* (ca. 14.5 mm body length: Thorell 1890). As *H. hosei* could be confused with the new species due to similar size, it is diagnosed and illustrated below.

METHODS

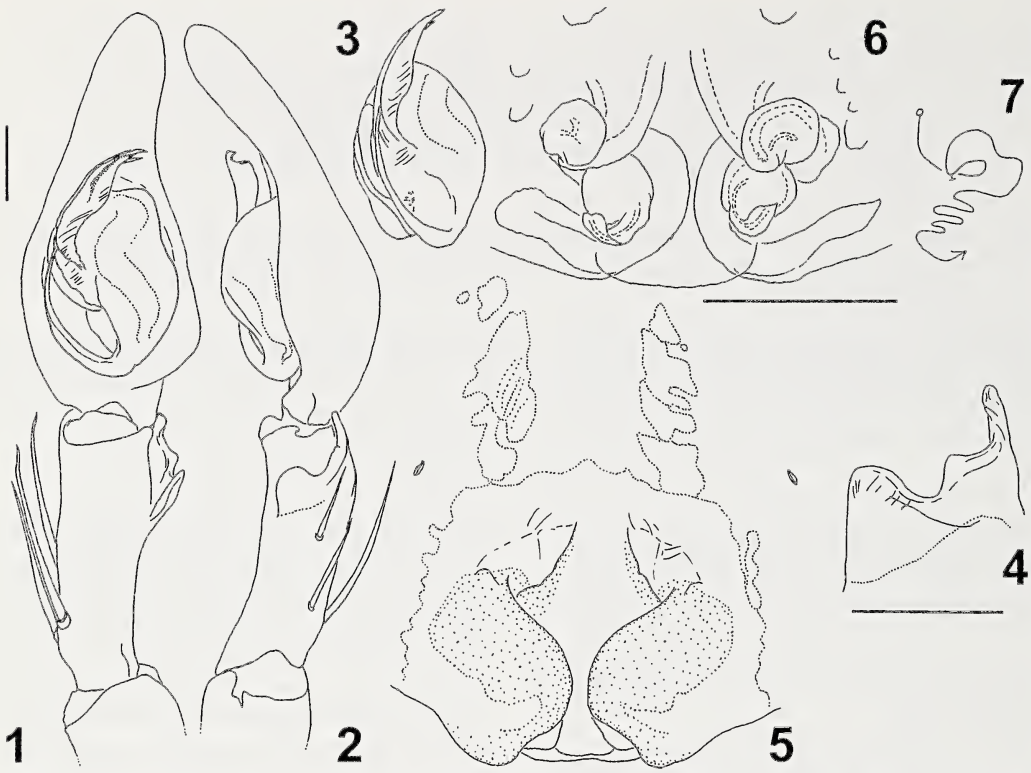
Specimens are deposited in the Field Museum of Natural History Chicago, USA (FMNH), Forschungsinstitut und Naturmuseum Senckenberg, Germany (SMF) and the Natural History Museum London, England (BMNH). Format and style of description as well as treatment of female genitalia follow Davies (1994) and Jäger (2000). Measurements are expressed in millimeters. Measurements of appendages are listed as: total length (femur, patella, tibia, metatarsus, tarsus). Arising points of tegular parts (i.e. embolus, conductor) are described for the left palp in a ventral view.

Abbreviations. ALE = anterior lateral eyes, AME = anterior median eyes, AW = anterior width of dorsal shield of prosoma, CH = clypeus height, FE = femur, MT = metatarsus, OL = opisthosoma length, OW = opisthosoma width, PA = patella, PH = height of dorsal shield of prosoma, PJ xx = serial number of Sparassidae examined by Peter Jäger, PL = length of dorsal shield of prosoma, PLE = posterior lateral eyes, PME = posterior median eyes, PP = palpus, PW = width of dorsal shield of prosoma, RTA = retrolateral tibal apophysis, TA = tarsus, TI = tibia, I/II/III/IV = leg I, etc.

TAXONOMY

Family Sparassidae Bertkau 1872
Genus *Heteropoda* Latreille 1804
Heteropoda natans new species
(Figs. 1–7)

Types.—Male holotype (PJ 1173), female paratype (PJ 1174): Malaysia, Borneo, Sabah, Kinabalu Park, near Poring, Hot Springs, Lowland Rainforest, stream edges, 6°03′N, 116°42′E, Airamé & Sierwald leg. IV-VI.1998



Figures 1–7.—*Heteropoda natans* new species: 1—2. left male palp; 1. ventral view; 2. retrolateral view; 3. left male bulb, prolateral view; 4. RTA, retrolateral view; 5. epigyne, ventral view; 6. vulva, dorsal view; 7. schematic course of internal duct system. Scale bars = 1 mm.

(FMNH 18975, 18972). Male paratype (PJ 1786): Malaysia, Borneo, Sabah, Kinabalu Park, near Poring Hot Springs. 6°03′N, 116°42′E, along river, 600m, *Heteropoda* male, P. Sierwald det. 1998 (SMF). Female paratype (PJ 1785): same data, *Heteropoda* female, P. Sierwald det. 1998 (SMF).

Etymology.—The specific name refers to the ability of this species to hunt on the water surface and to dive and hide under water (Latin: *natans* = swimming), adjective.

Diagnosis.—Tip of conductor divided into two parts as in *H. squamacea* Wang 1990 from southern China (see Wang 1990: figs. 6, 7), but male dorsal RTA of *H. natans* with a distinct protrusion between dorsal and ventral part (Fig. 4). Retrolateral margin of conductor undulating. Females with slightly rectangular epigynal field, this with distinct anterior bands. Lateral lobes not touching each other. Median septum anteriorly trapezoid. Spermathecae almost as large as anterior coils of copulatory ducts.

Description.—*Male holotype (PJ 1173):* PL 10.6, PW 10.2, AW 4.6, PH 2.6, OL 10.5, OW 6.8. Eyes: AME 0.51, ALE 0.71, PME 0.56, PLE 0.71, AME-AME 0.30, AME-ALE 0.08, PME-PME 0.42, PME-PLE 0.66, AME-PME 0.52, ALE-PLE 0.53, CH AME 0.98, CH ALE 0.77. Leg formula: 2143, spination: PP 131,101,2120, FE I-II 323, III 333, IV 331, PA 101, TI I-II 2326, III 2226, IV 2126, MT I-II 1014, III 2014, IV 3036. Leg measurements: PP 17.4 (5.9, 2.6, 3.4, -, 5.5), I 70.8 (18.5, 6.5, 21.1, 19.6, 5.1), II 82.2 (22.0, 6.7, 24.3, 23.7, 5.5), III 62.4 (17.6, 5.9, 18.5, 16.3, 4.1), IV 69.9 (19.6, 5.5, 19.6, 20.5, 4.7).

Chelicerae with 5–6 posterior teeth. Organization of palpal structures simple, i.e. embolus arising in a 6-o'clock-position on the tegulum, following a semi-circular path. Conductor arising in a 9:30-o'clock-position on the tegulum. Sperm duct shaped like broad 'S' across the tegulum.

Color: Reddish-brown to brown with dark markings, made up of short dark hairs. Chelicerae reddish-brown with three longitudinal bands. Prosoma with dark radial markings and

a white 'V'-shaped line, consisting of white short hairs, running along the suture between head and thoracical region. Sternum, gnathocoxae, labium, ventral coxae and trochanter pale brown without markings. Opisthosoma covered with dark hairs. Ventral opisthosoma with a light yellowish-brown median band.

Female paratype (PJ 1174): PL 14.9, PW 13.2, AW 6.5, PH 4.1, OL 19.2, OW 12.6. Eyes: AME 0.47, ALE 0.78, PME 0.63, PLE 0.77, AME-AME 0.57, AME-ALE 0.20, PME-PME 0.66, PME-PLE 0.86, AME-PME 0.77, ALE-PLE 0.80, CH AME 1.40, CH ALE 1.12. Leg formula: 2413, spination: PP 131,101,2(1)121,1014(3), FE I-II 323, III 333, IV 331, PA 101, TI I 21(2)26, II-IV 2126, MT I-II 1014, III 2014, IV 3036. Palpal claw with 8 teeth. Leg measurements: PP 22.9 (6.7, 3.2, 5.2, -, 7.8), I 71.9 (20.1, 7.4, 21.2, 18.5, 4.7), II 79.3 (22.7, 7.9, 23.5, 20.2, 5.0), III 65.6 (19.5, 7.1, 18.7, 16.2, 4.1), IV 75.4 (21.1, 7.0, 21.5, 20.7, 5.1).

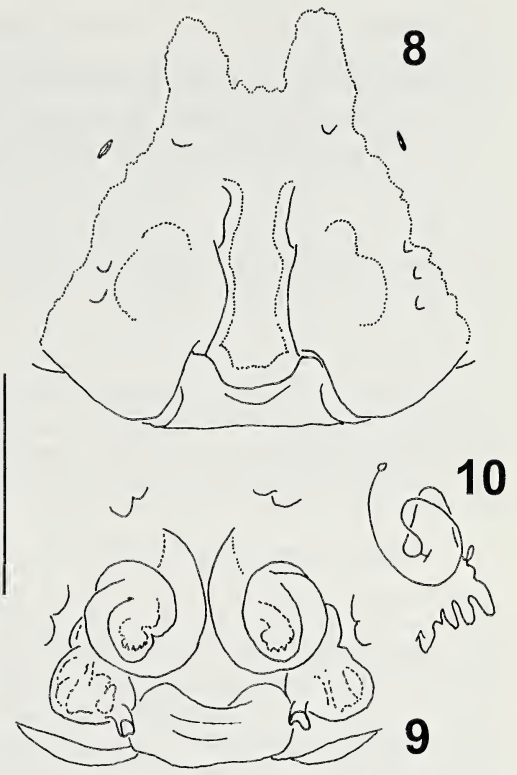
Chelicerae with 5 posterior teeth. Lateral lobes of epigyne broad tongue-shaped, covering mainly posterior parts of the median septum. Anterior bands of epigynal field fragmented. Spermathecae separated from each other by one of their diameters. Slit sense organs separated 2.5–4 times of their length from epigynal field (Fig. 5).

Color: As in male, but generally darker (i.e. reddish-brown). Prosoma and opisthosoma covered continously with dark hairs, without any pattern.

Variation.—*Male paratype (PJ 1786):* PL 11.6, OL 12.1; *female paratype (PJ 1785):* PL 13.7, OL 12.4.

Distribution.—Only known from the type locality.

Biology.—Observations on the biology of *Heteropoda natans* were made and published by Airamé & Sierwald (2000). Specimens were found sitting at the edge of streams. One specimen was observed jumping into the water and diving. In the laboratory, feeding experiments showed that individuals of *H. natans* monitor for prey by holding their pedipalps and the first two pairs of legs in the water. From the prey offered to the spiders (cockroaches, fish, large and small tadpoles) only tadpoles were rejected under laboratory conditions. In these experiments cockroaches were the preferred prey.



Figures 8–10.—*Heteropoda hosei* Pocock 1897: 8. epigyne, ventral view; 9. vulva, dorsal view; 10. schematic course of internal duct system. Scale bar = 1 mm.

Heteropoda hosei Pocock 1897
(Figs. 8–10)

Heteropoda hosei Pocock 1897: 614, figs. 21–21a; 1 female syntype (PJ 1765): Malaysia, Sarawak, purchased E. Gerrara, (BMNH 1894.9.19.11–31). Examined and herewith designated as lectotype (see Remarks below).

Diagnosis.—Epigynal field roughly trapezoid with short anterior bands, these neither fragmented nor separated from the field. Median septum covered only on its margins by lateral lobes. Posterior margin of median septum distinctly separated from the epigastric furrow. Spermathecae separated from each other by at least 1.5 times their diameters, extending laterally beyond the first windings of the internal duct system.

Description.—PL 10.0. Slit sense organs separated by their length from the epigynal field (Fig. 8). For further details see Pocock (1897).

Distribution.—Only known from the type locality (Sarawak).

Remarks.—Pocock (1897) mentioned two female specimens in his original description, one from Baram River in Borneo and one from Sarawak. These have to be considered syntypes. In the BMNH only one series of *H. hosei* was found. It comprises three adult females and one subadult female from Sarawak. One adult female is labelled as type, matches with the original description (the other specimens are smaller and probably added later to the vial) and is considered belonging to the syntype series. The other syntype was not found and its whereabouts remain unkown. To support stability the only located syntype (PJ 1765) is herewith designated as lectotype.

ACKNOWLEDGMENTS

Parts of this research arose from a visit to the BMNH, which was sponsored by the European Community (Access to Research Infrastructure action of the Improving Human Potential Programme: London—SYS-RESOURCE program). Thanks go to Satie Airamé and Petra Sierwald (both Chicago) for collecting and providing the specimens and to an anonymous referee and Mark Harvey for improving the manuscript with helpful comments.

LITERATURE CITED

Airamé, S. & P. Sierwald. 2000. Hunting and feeding behavior of one *Heteropoda* species in lowland rainforest on Borneo (Araneae, Sparassidae). Journal of Arachnology 28(2):251–253.

Davies, V.T. 1994. The huntsman spiders *Heteropoda* Latreille and *Yiinthi* gen. nov. (Araneae: Heteropodidae) in Australia. Memoirs of the Queensland Museum 35(1):75–122.

Jäger, P. 2000. Two new heteropodine genera from southern continental Asia (Araneae: Sparassidae). Acta Arachnologica 49(1):61–71.

Jäger, P. 2002. Heteropodinae: transfers and synonymies (Arachnida: Araneae: Sparassidae). Acta Arachnologica 51(1):33–61.

Pocock, R.I. 1897. Spinnen (Araneae). *In* Ergebnisse einer zoologischen Forschungsreise in den Molukken und Borneo. (Kükenthal, W. ed.). Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 33(4):591–629.

Thorell, T. 1890. Diagnoses Aranearum aliquot novarum in Indo-Malesia inventarum. Annali del Museo Civico di Storia Naturale di Genova (2) 10:132–172.

Wang, J.-F. 1990. Six new species of the spiders of the genus *Heteropoda* from China (Araneae: Heteropodidae). Sichuan Journal of Zoology 9(3):7–11.

Manuscript received 11 February 2004, revised 4 May 2004.

2005. The Journal of Arachnology 33:719–725

THREE NEW SPECIES OF SOLIFUGAE FROM NORTH AMERICA AND A DESCRIPTION OF THE FEMALE OF *BRANCHIA BREVIS* (ARACHNIDA, SOLIFUGAE)

Jack O. Brookhart and **Paula E. Cushing**: Department of Zoology, Denver Museum of Nature & Science, 2001 Colorado Blvd., Denver, Colorado 80205-5798, USA. E-mail: joipbroo@comcast.net

ABSTRACT. Three new species of Solifugae are described: *Eremobates paleta* from Mexico, is a member of the *Eremobates scaber* species group; *Eremobates inkopaensis* from California, U.S.A., is a member of the *Eremobates palpisetulosus* group; and *Eremochelis albaventralis* from Mexico is tentatively placed in the *Eremochelis bilobatus* group. The female of *Branchia brevis* Muma from Texas, U.S.A. is described for the first time.

Keywords: Solpugida, species description, taxonomy, camel spider, sun spider, wind scorpion

New species of solifugids are being discovered each year as a result of re-examination of museum material and newly collected material being sent in for identification. These new species are beginning to shed some light on the phylogenetic relationships among species and between species-groups (Brookhart & Cushing 2002, 2004). Herein we describe three new species in the family Eremobatidae and provide a description of the female of *Branchia brevis* Muma 1951 from the family Ammotrechidae.

Using the methods of Muma (1951), Brookhart & Muma (1981, 1987), Muma & Brookhart (1988) and Brookhart & Cushing (2002, 2004) we measured length of palpus, leg I, leg IV, length and width of chelicera and propeltidium, length and width of fondal notch when present, width of base of fixed finger, and length and width of female genital operculum. Abbreviations used to indicate various cheliceral structures are as follows: FF = fixed finger; MF = movable finger; PT = primary tooth; AT = anterior tooth; MT = medial tooth; IT = intermediate tooth; MST = mesal tooth. All measurements are in millimeters.

The number, shape and relative length of ctenidia to succeeding tergite was noted. Counts were made of palpal papillae. Color of palpus, legs I, II, III, IV and general overall color especially that of the propeltidium was recorded. The shape of the female genital operculum especially the medial margin was observed using the terminology of Brookhart & Cushing (2004).

Ratios used previously by Muma (1951, 1970, 1989), Brookhart & Muma (1981, 1987), Muma & Brookhart (1988), and Brookhart & Cushing (2002) were computed. These ratios are as follows: A/CP: the sum of the lengths of palpus, leg I, and leg IV divided by the sum of length of chelicera and propeltidium indicating length of appendages in relation to body size. The larger the number, the longer legged is the species. CL/CW: cheliceral length divided by cheliceral width. FL/FW indicates whether the cheliceral fondal notch is longer or wider. Longer is defined as the anterior to posterior axis and width is defined as the dorsal to ventral axis. PL/PW compares propeltidium length to width. FW/FFW diagnoses the size of fondal notch compared to the thickness of fixed finger. CW/FFW is used to indicate whether the fixed cheliceral finger is thin or robust in relation to the size of the chelicera. This is a useful ratio when there is no fondal notch. GOL/GOW demonstrates the relative size of the female genital operculum in terms of length and width. Abbreviations for collections are as follows: DMNS = Denver Museum of Nature & Science, Denver, Colorado; EMEC = Essig Museum of Entomology, University of California at Berkeley, Berkeley, California; FSCA = Florida State Collection of Arthro-

pods, Gainesville, Florida; SDMC = San Diego Natural History Museum, San Diego, California.

SYSTEMATICS

Family Eremobatidae Kraepelin 1901
Subfamily Eremobatinae Kraepelin 1901
Genus *Eremobates* Banks 1900

Eremobates paleta new species
Figs. 1–5

Material examined.—Holotype male from 2.5 km S. of El Salto (23°28′N, 105°13′W), *Durango Province,* Mexico, 4 August 1986, D.K. Faulkner (SDMC).

Etymology.—From the Spanish for trowel, *paleta,* which refers to the shape of the four ctenidia. To be treated as a noun in apposition.

Diagnosis.—This new species is placed in the *Eremobates scaber* group based on the notch on the posterior aspect of the male fixed finger when viewed dorsally. The four trowel-shaped ctenidia as well as the combination of coloration and "crimped" male fixed finger distinguishes it from other members of the *Eremobates scaber* group.

Description.—*Male holotype:* total length 20, chelicera length 2.5, chelicera width 2.5, propeltidium length 3.5, propeltidium width 4.8, palpus length 16, first leg length 17, fourth leg length 20. Ratios: A/CP 8.8, CL/CW 2.24, PL/PW 0.73, FL/FW 1.0, CW/FFW 5.0.

Overall coloration lemon yellow with dusky purplish-brown markings on anterior edge of propeltidium and ocular area (Fig. 1), violet-brown on apical tip of palpal tarsus (Fig. 2). All legs lemon yellow, abdomen dark violet brown dorsally, lighter violet brown ventrally, pleura a light violet. Malleoli white. Cheliceral fixed finger "crimped" in mesal view without teeth, movable finger with large PT, smaller AT with no cleft, posterior IT on PT, MST medium in size. "Crimped" fixed finger defined in Brookhart & Cushing (2004) and shown as a recurved dorsal edge of fixed finger in Fig. 3. Fondal notch equal in length to width. Fondal teeth graded I, III, II, IV ectally and mesally (Figs. 3 & 4). Mesoventral groove typical of the group, narrow, deep, ending in a cup-like depression beneath the origins of flagellum complex. Flagellum complex typical of *Eremobates* group with apical plumose bristle large, flattened, occupying approximately 90% of mesoventral groove. Palpus with 40 rounded papillae on the apical, ventral region of palpus (Fig. 2). Four short, trowel shaped ctenidia (Fig. 5).

Remarks.—The only valid recorded member of the scaber group from Mexico is *Eremobates legalis* Harvey 2002 which is known from the female type only and has no type locality. Vásquez-Rojas's (1981, 1995) records of *Eremobates zinni* Muma 1951 and *Eremobates ctenidiellus* Muma 1951 appear to be in error based on our recent studies (Brookhart & Cushing 2004). *Eremobates paleta* does not appear to be related to *E. legalis* based on coloration. Gavino (pers. comm.) is also describing a new scaber species from the Baja region of Mexico. The "crimped" aspect of the fixed finger is unusual for a species in the southern regions of North America (Brookhart & Cushing 2004).

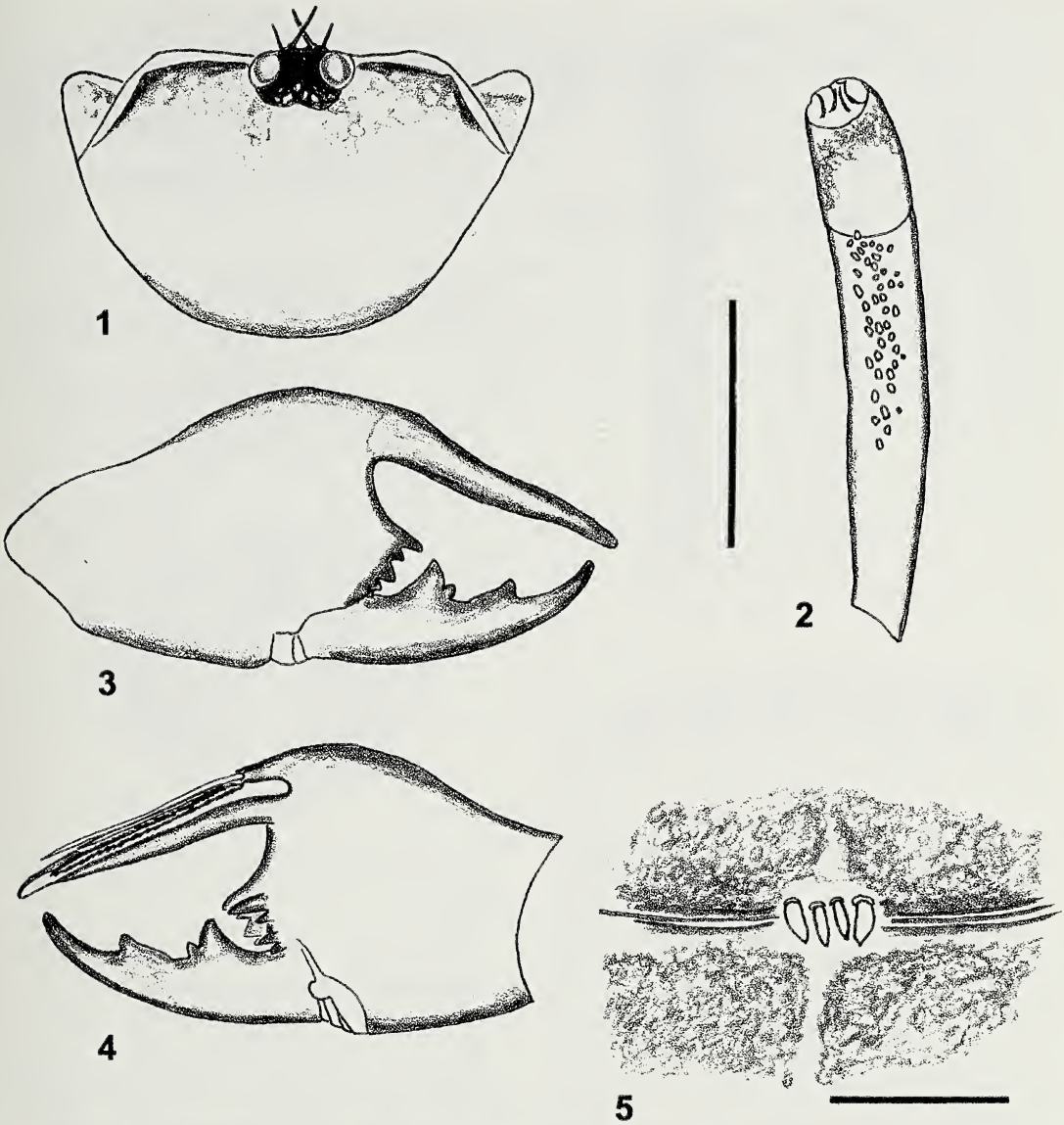
Eremobates inkopaensis new species
Figs. 6–9

Material examined.—Male holotype, In Ko Pah Valley, Meyer Gorge (32°43′N, 116°02′W), Imperial County, *California*, U.S.A., 14 March 1982, pitfall trap, J. Berrian (SDMC). Female allotype from same site, pitfall trap, 17 April 1982, J. Berrian (SDMC). Paratypes: U.S.A.: *California*: 6 males and 1 female from same site locality by same collector between 4 March–17 April 1982 (5 male paratypes in SDMC, 1 male and 1 female in DMNS).

Etymology.—Refers to the type locality, In Ko Pah Valley.

Diagnosis.—This member of the *Eremobates palpisetulosus* group is a member of the kraepelini series as defined by Muma & Brookhart (1988). It is the only member of this group without ctenidia. Most members of this series are pale but have some dusky to dusky purple markings. *Eremobates inkopaensis* is entirely pale in both the male and female.

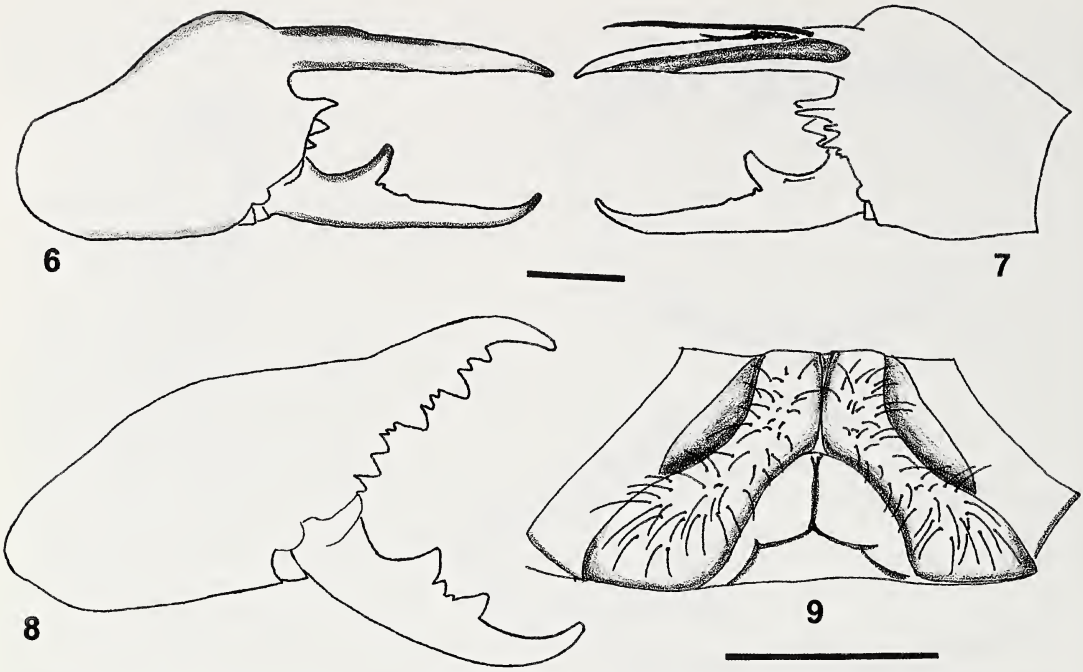
Description.—*Male holotype:* total length 21, cheliceral length 5.4, cheliceral width 2.2, propeltidium length 2.6, propeltidium width 5.2, palpus length 14, first leg length 16, fourth leg length 27. Ratios: A/CP 7.04, CL/CW 2.6, PL/PW 0.5, FL/FW 1.0, CW/FFW 5.2. Coloration cream yellow in all aspects of chelicera, propeltidium and appendages. Malleoli white. Cheliceral FF with low, incon-



Figures 1–5.—*Eremobates paleta* new species. 1–5. Male holotype. 1. Male propeltidium, dorsal view; 2. Male palpus, ventral view; 3. Male right chelicera, ectal view; 4. Male right chelicera, mesal view; 5. Male fourth abdominal segment showing ctenidia, ventral view. Scale bars = 1 mm.

spicuous ridge on basal aspect of FF. No teeth ventrally. MF with large PT but only a low ridge anteriorally, small posterior IT separate from PT, tiny AT, MST absent (some paratypes have tiny MST). Fondal teeth graded I, III, II, IV. Fondal notch equal length to width. Mesoventral groove deep, median in position expanding ventrally near the tip (Figs. 6 & 7). Flagellum complex typical of group, no ctenidia, no palpal papillae. *Male paratypes (6):* total length 20–26, cheliceral length 5.5–6.4, cheliceral width 2.2–2.9, propeltidum length 2.3–3.1, propeltidium width 4.4–4.9, palpus length 17.5–22.0, first leg length 16.0–18.0, fourth leg length 22.0–29.0. Ratios: A/CP 6.5–8.0, CL/CW 2.2–2.9, PL/PW 0.52–0.67, FL/FW 0.7–1.0, CW/FFW 4.2–4.8.

Female allotype: total length 22, cheliceral length 6.2, cheliceral width 2.2, propeltidium length 2.1, propeltidum width 3.9, palpus



Figures 6–9.—*Eremobates inkopaensis* new species. 6–7. Male holotype. 6. Male right chelicera, ectal view; 7. Male right chelicera, mesal view. 8–9. Female allotype. 8. Female right chelicera, ectal view; 9. Female genital operculum, ventral view. Scale bar = 1 mm.

16.5, first leg length 12.5, fourth leg length 21.0. *Ratios*: A/CP 4.3, CL/CW 2.8, PL/PW 0.74 GOL/GOW 0.82. Coloration is the same as the males. Chelicera typical of the group, FF with large PT and MT, smaller AT, two IT between PT and MT, one IT between IT and AT, MF with large PT and medium AT, two smaller IT, MST absent (Fig. 8). Genital opercula with broad anterior arms, recurved medial margin, short, curved wings, posterior margin straight (Fig. 9). The allotype but not the paratype with four tiny, thin ctenidia. *Female paratype (1)*: total length 31, cheliceral length 6.8, cheliceral width 2.2, propeltidium length 3.7, propeltidium width 5.5, palpus length 19.5, first leg length 16.5, fourth leg length 26.0. *Ratios*: A/CP 5.96, CL/CW 2.6, PL/PW 0.65, GOL/GOW 0.76.

Remarks.—The nine specimens of *Eremobates inkopahensis* were collected in mid-March to early April indicating an early maturity. *Eremobates gracilidens* Muma 1951 is also found in southern California in Inyo and San Bernardino counties. The two females are shorter legged then *E. gracilidens* based on the A/CP ratio. The genital opercula are typical of the group although the anterior arms are broader than in other members of this group.

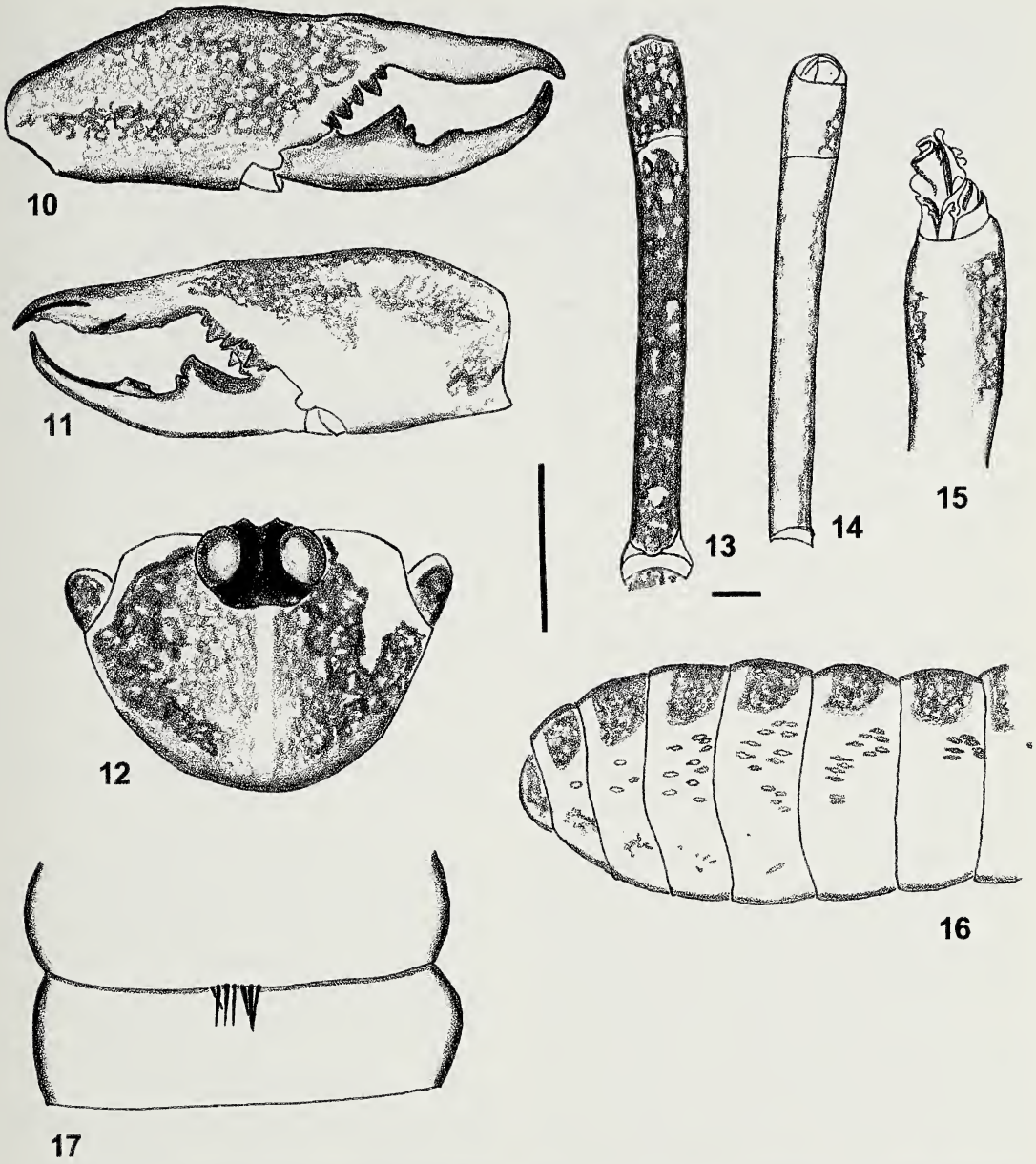
Genus *Eremochelis* Roewer 1934
Eremochelis albaventralis new species
Figs. 10–17

Material examined.—Holotype male, 7 km WSW of Juchitepec (19°06′N, 98°52′W), *Mexico State,* Mexico, 24 August 1987, J. Doyen (CAS). Paratypes: Mexico: *Mexico State*: 1 male, same collection data as holotype (CAS); 1 male, same collection data as holotype (DMNS).

Etymology.—Refers to the contrasting white underside of the species.

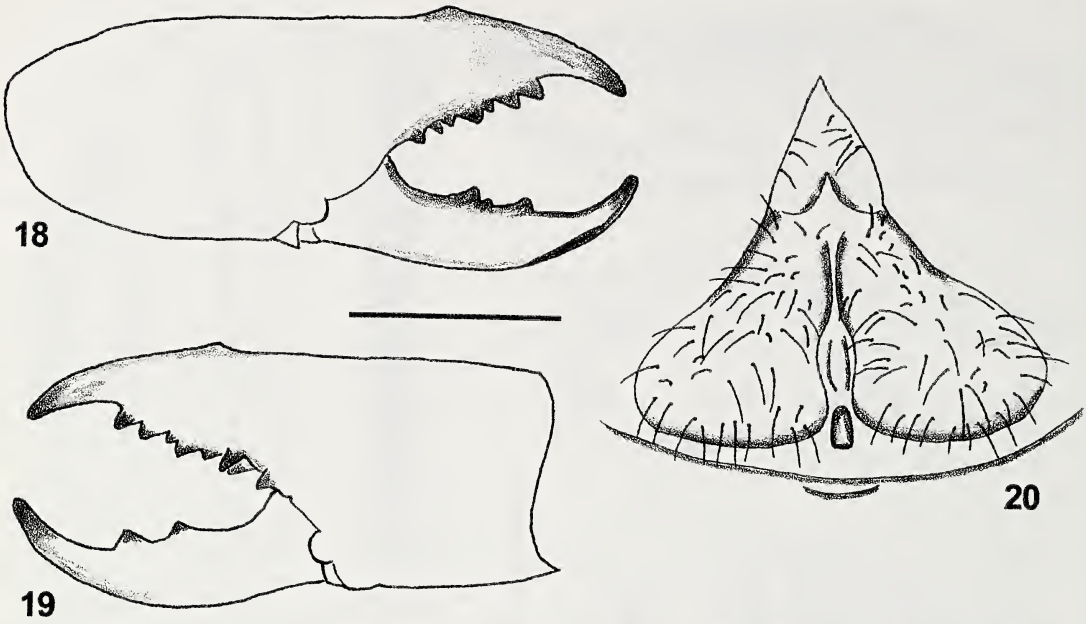
Diagnosis.—This species is distinguished from *Eremochelis rossi* Muma 1987 on the basis of coloration, shape of fixed finger, and ctenidial number and shape.

Description.—*Male holotype:* total length 14, cheliceral length 3.3, cheliceral width 1.3, propeltidium length 1.5, propeltidium width 2.3, palpus length 13.5, first leg length 10.0, fourth leg length 14.0. Ratios: A/CP 7.8, CL/CW 2.5, PL/PW 0.43, no fond, CW/FFW 2.6.



Figures 10–17.—*Eremochelis albaventralis* new species. 10–14. Male holotype. 10. Male right chelicera, ectal view; 11. Male right chelicera, mesal view; 12. Male propeltidium, dorsal view; 13. Male right palpus, dorsal view; 14. Male right palpus, ventral view. 15. Male paratype, ventral view showing everted suctorial organ. 16–17. Male holotype. 16. Male abdomen, ectal view; 17. Male fourth abdominal segment showing ctenidia. Vertical scale line = 1 mm for 10, 11, 12, 16, & 17. Horizontal scale line = 1 mm for 13, 14, & 15.

Metatarsus/tarsus ratio 4.2. *Male paratypes (2):* total length 13–15, cheliceral length 3.4–3.6, cheliceral width 1.3–1.6, propeltidum length 1.9–2.0, propeltidium width 2.3–2.7, palpus length 13.0–16.0, first leg length 10.0–11.0, fourth leg length 14.0–17.0. *Ratios*: A/CP 6.2–7.0, CL/CW 2.25–2.40, PL/PW 0.75–0.80, no fond, CW/FFW 2.6–3.2. Metatarsus/tarsus ratio 4.25–4.50. Coloration in alcohol a blotchy, vibrant violet brown on the dorsal as-



Figures 18–20.—*Branchia brevis* female. 18. Female right chelicera, ectal view; 19. Female right chelicera, mesal view; 20. Female genital operculum, ventral view. Scale line = 1 mm.

pect of most of palpus (Fig. 13), legs I, II, III, IV and most of the propeltidum except for a thin linear area of creamy yellow on the median sector (Fig. 12). Entire ventral aspect white including palpus (Fig. 14). Abdomen more lightly colored with distinct patches on the ectal regions (Fig. 16). Chelicera with 3 lighter stripes ectally of the same color (Fig. 10). Malleoli white. Cheliceral FF with no teeth or denticles, blade shaped with a circular region where you would normally find the fondal notch. Small ventral cup anteriorly extending to a broad, shallow mesoventral groove. MF with large PT and a cusp-like structure for an AT; small IT on the PT; no MST (Figs. 10 & 11). Flagella complex of tubular to slightly striate bristles. No scopula, seven short, needle-like ctenidia (Fig. 17). The everted palpal suctorial organ is shown in Fig. 15.

Remarks.—This species is tentatively placed in the *Eremochelis bilobatus* group but clearly needs to be part of a new group which would include *E. albaventralis*, *E. rossi* Muma 1987, *E. cochiseae* Muma 1989, *E. kerni* Muma 1989 and possibly the two members of the *E. andreasana* group, *E. andreasana* Muma 1962 and *E. larrea* Muma 1962. This distinction is based mainly on the unique shape of the male chelicera.

Family Ammotrechidae Roewer 1934
Subfamily Saronominae Roewer 1934
Genus *Branchia* Muma 1951
Branchia brevis Muma 1951
Figs. 18–20

Branchia brevis Muma 1951: 137–138, figs. 311, 312; Harvey 2003: 208 (full synonymy).

Type specimen.—Holotype male, Edinburgh, Hidalgo County, *Texas*, U.S.A. (26°11′N, 98°06′W), 15 March 1939, S. Mulaik (AMNH).

Material examined.—U.S.A.: *Texas:* Webb County: 19 ♂, 8 ♀, 57.1 km NW of Laredo (27°34′N, 99°30′W), Rt. 83, under cow pies, 21 April 1980, M.H. Muma (FSCA); 2 ♂, 1 ♀, same collection data (DMNS).

Description.—*Females (5):* Length 16.0–18.5, cheliceral length 2.8–3.3, cheliceral width 1.1–1.2, propeltidium length 1.8–2.1, propeltidium width 1.9–2.3, palpus length 5.0–7.0, first leg length 4.0–5.0, fourth leg length 11.5–12.5. Ratios: A/CP 4.45–4.53, PL/PW 0.9, GOL/GOW 0.85–0.92.

Overall coloration in alcohol pale creamy

yellow; ocular area pale; palpus with splotchy brown violet on tarsus and apical two thirds of metatarsus; other appendages creamy yellow; abdomen dusky yellow dorsally and very pale ventrally. Fixed finger typical of the group with equally sized PT, MT and AT; one small IT between PT and MT, MST absent; FT graded II, I ectally and III mesally (Figs. 18 & 19). No ctenidia, no palpal papillae. Genital operculum typical of the group (Fig. 20).

Remarks.—Muma (1951) described the male of *Branchia brevis* from Hidalgo Texas, U.S.A. but did not describe a female allotype (Muma 1951, 1962, 1970, 1989). One of the authors (JOB) has in his personal collection two males and a female from 57.1 km northwest of Laredo, Texas labeled "*Branchia brevipes*" with the Muma identifying label. There is no record of this species. The FSCA also has five vials containing nineteen males and eight females of Muma's material from the same site collected on the same day labeled "*Branchia brevipes*". Examination of the male holotype as well as the above material determined all these specimens to be *Brancia brevis* Muma. These are included in the material examined.

ACKNOWLEDGMENTS

We would like to thank Lorenzo Prendini (AMNH); Cheryl Barr (EMEC); Paisley Cato and Jim Berrian (SDMC); and G.B. Edwards (FSCA) for loaning the specimens used in this study. This project was partially supported by National Science Foundation grant DBI-0346378 awarded to PEC.

LITERATURE CITED

Brookhart, J.O. & P.E. Cushing. 2002. New species of Eremobatidae (Arachnida, Solifugae) from North America. Journal of Arachnology 30:84–97.

Brookhart, J.O. & P.E. Cushing. 2004. The systematics of the *Eremobates scaber* species-group (Solifugae, Eremobatidae). Journal of Arachnology 32:284–312.

Brookhart, J.O. & M.H. Muma. 1981. The *pallipes* species-group of *Eremobates* Banks (Solpugida: Arachnida). Florida Entomologist 64:283–308.

Brookhart, J.O. & M.H. Muma. 1987. *Arenotherus*, a new genus of Eremobatidae (Solpugida) in the United States. Printed for the authors by Cherry Creek High School Print Shop, Englewood, Colorado.

Harvey, M.S. 2002. Nomenclatural notes on Solifugae, Amblypygi, Uropygi and Araneae (Arachnida). Records of the Western Australian Museum 20:449–459.

Harvey, M.S. 2003. Catalogue of the Smaller Arachnid Orders of the World: Amblypygi, Uropygi, Schizomida, Palpigradi, Ricinulei and Solifugae. CSIRO Publishing, Melbourne.

Muma, M.H. 1951. The arachnid order Solpugida in the United States. Bulletin of the American Museum of Natural History 97:35–141.

Muma, M.H. 1962. The arachnid order Solpugida in the United States, supplement 1, American Museum Novitates 2092:1–44.

Muma, M.H. 1970. A synoptic review of North American, Central American and West Indian Solpugida (Arthropoda: Arachnida): Arthropods of Florida and Neighboring Land Areas 5:1–62.

Muma, M.H. 1989. New species and records of Solpugida (Arachnida) from the United States. Privately published by the author by Douglas Print Shop. Pp. 1–50.

Muma, M.H. & J.O. Brookhart. 1988. The *Eremobates palpisetulosus* species-group (Solpugida: Eremobatidae) in the United States. Published for the authors by the Cherry Creek High School print shop.

Roewer, C.F. 1934. Solifugae, Palpigradi. Vol. 5(IV)(4)(4–5). Pp. 481–723. *In* Klassen und Ordnungen des Tierreichs. 5: Arthropoda. IV: Arachnoidea (Bronn, H.G., Ed.), Akademische Verlagsgesellschaft M.B.H., Leipzig.

Vázquez-Rojas, I.M. 1981. Solifugos de México (Arachnida: Solifugae). Universidad Nacional Autónoma de México, Facultad de Ciencias, México (D.F.) Pp. 1–78. Bachelor of Science Thesis. Unpublished.

Vázquez-Rojas, I.M. 1995. Los arácnidos de México parte 1: Ricinulei, Amblypygi, Solifugae, Palpigradi, Schizomida, Uropygi. Dugesiana 2: 15–17.

Manuscript received 17 December 2003, revised 17 June 2004.

2005. The Journal of Arachnology 33:726–734

VISUAL ACUITY OF THE SHEET-WEB BUILDING SPIDER *BADUMNA INSIGNIS* (ARANEAE, DESIDAE)

Christofer J. Clemente, Kellie A. McMaster, Liz Fox, Lisa Meldrum[1], **Barbara York Main** and **Tom Stewart**: School of Animal Biology, University of Western Australia, Crawley, Western Australia, 6009.

ABSTRACT. Visual acuity in the sheet-web building spider *Badumna insignis* (L. Koch 1872) (Araneae, Desidae) was examined in relation to its microhabitat. We examined, using histological techniques, the major structural and functional features of the visual systems, including external and internal ocular organizations, resolution, sensitivity, focal lengths and the field of view for each eye. *Badumna insignis* showed little differentiation in its ocular arrangement from the presumed ancestral condition in spiders, with poor visual acuity and a small field of view. Resolution and sensitivity were low, particularly in the secondary eyes. The AM eyes were enhanced showing larger fields of view and higher sensitivity, resembling that of nocturnal uloborids. These eyes appear adapted for close-range recognition, due to short-range focus and good visual overlap.

Keywords: Corneal eye, vision, field of view, sheet-web

Spiders are renowned for their effective and complex visual systems (Land 1985). The primitive eye arrangement of spiders, as hypothesized by Homann (1971), consists of two transverse rows each containing four eyes. The first row consists of the anterior median (AM) eyes in the middle and the anterior lateral (AL) eyes on the periphery. Similarly, the posterior eyes are grouped into posterior median (PM) eyes and posterior lateral (PL) eyes. However, deviations from this pattern are common in extant species. The eyes of spiders often form three or four rows and certain pairs of eyes may become specialized and enlarged, while other pairs may become reduced or lost (Homann 1971; Comstock 1948). The visual capacity of spiders varies according to the size, shape, internal arrangement and position of the visual field of the eyes (Forster 1979; Foelix 1982; Opell & Cushing 1986; Opell & Ware 1987; Land & Barth 1992).

Visual acuity is a combination of many aspects of the visual system such as field of view, focal length, resolution and sensitivity. The external placement and internal arrangement determine the field of view of each eye (Land 1985). Forward-facing binocular vision is a product of overlapping visual fields, and is necessary for good distance judgment. The distance over which an eye can focus upon an object is determined by the focal length of its lens (Homann 1971). This ranges from 38.01 μm in the AL eyes of the uloborid *Hyptiotes cavatus* (Hentz 1847) (although this eye appears to be vestigial; Opell & Ware 1987), to 448 μm in the PM eyes of the ctenid *Cupiennius salei* (Keyserling 1877) (Land & Barth 1992). Sensitivity, or the ability to see in low light levels varies, generally in relation to the light conditions under which each species operates (Opell & Ware 1987). The number of visual cells (rhabdomeres) within the retina determines the quality of image resolution (Foelix 1982). Small numbers of rhabdomeres in the retina, such as 10–20 in some eyes of the ochyroceratid *Speocera* (Berland 1914), detect little more than movement (Homann 1971). In contrast, the PM eyes of the wolf spider *Lycosa tarantula* (Linnaeus 1758), contain about 5470 rhabdomeres and would thus have greater image resolution (Kovoor et al. 1992).

Visual acuity in a spider is often related to the microhabitat that it occupies, or the type of prey and method of capture (Forster 1979; Rovner 1993; Schmid 1998; Ortega-Escobar & Munoz-Cuevas 1999). However, much of the literature is limited to spiders in relatively few microhabitat types, such as salticids, ac-

[1] Deceased.

tively-hunting jumping predators (Land 1969; Forster 1979; Harland & Jackson 2000 2002; Parker & Hegedus 2003); lycosids, ground dwelling sit-and-wait predators (Lizotte & Rovner 1988; Land & Barth 1992; Rovner 1993; Persons & Uetz 1996, 1998; Grusch et al. 1997; Schmid 1998; Ortega-Escobar & Munoz-Cuevas 1999; Dacke et al. 2001); uloborids, orb web or single line web building spiders (Opell & Cushing 1986; Opell & Ware 1987; Opell 1988) and *Deinopis subrufa* (L. Koch 1879), a net casting spider (Blest & Land 1977). Few studies have focused on visual acuity in a sheet-web building spider.

We examined the focal length, resolution, sensitivity and field of view in *Badumna insignis* (Koch 1872), which builds an asymmetrical sheet-web that extends from a tubular retreat and is attached to a substrate. The web consists of many pairs of parallel support lines overlain with zigzag threads of cribellate silk that function to entangle prey (Main 1976; Opell 1999). The sheet-web of *B. insignis* both defines the individual's foraging patch and provides some shelter from predators. Vibrations on the web can also be used to recognize the identity of an object (Suter 1978; Barth 1982; Masters et al. 1986; Herberstein et al. 1998). In natural situations *B. insignis* builds its web under the shelter of logs, loose bark of trees, rocks, cliffs and stones, preferring dry positions (Main 1964). However its opportunistic nature has allowed it to take advantage of areas settled by humans, where it is quite common around houses, sheds, window-sills, under eaves and rafters, boxes and outdoor furniture (Main 2001).

METHODS

Twenty adult female specimens of *Badumna insignis* (L. Koch 1872) were collected over a period of three weeks during February 2001, within the grounds of The University of Western Australia.

External ocular organization.—Three external features were measured on each specimen: total eye width (TEW), total eye depth (TED) and eye diameters (Fig. 1). These measurements may be influenced by both orientation of the lens and the amount of tissue devoted to each eye type. Measurements were taken under a binocular dissecting microscope with an ocular micrometer. Since all the external features correlated significantly with carapace length (with the exception of the diameter of the PM eyes $P = 0.054$), values were standardized for the animals' size by dividing each measurement by the carapace length. Repeated measures ANOVA with one within subject factor and no between subject factors, and Student-Newman-Keuls post-hoc tests, were used to determine significant differences in the relative eye diameters.

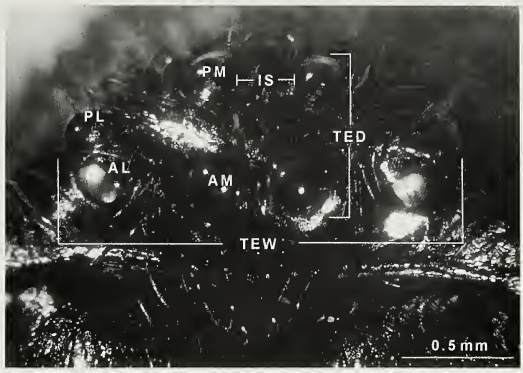


Figure 1.—External measurements taken on *B. insignis*; AM = anterior median eyes; AL = anterior lateral eyes; PM = posterior median eyes; PL = posterior lateral eyes; TED = total eye diameter; TEW = total eye width; IS = interocular space.

Internal ocular organization.—Three specimens of *B. insignis* were killed, using CO_2 gas, and the cephalathorax trimmed to a small block of tissue and fixed in Karnovsky's fixative for 72 hours. Specimens were then washed and further trimmed down in spider saline (scorpion saline excluding the $CaCl_2$; Zwicky 1968) and placed in phosphate buffer prior to being embedded in araldite/procure. Longitudinal and transverse sections (1 μm thick) were cut using an LKB ultratome and a diamond knife. Sections were mounted on slides and stained with toluidine blue. These sections were used to determine the internal ocular organization and to measure resolution, sensitivity and field of view of individual eyes.

Resolution.—The numbers of axons exiting each eye were counted from sections cut using the same methods as for internal ocular organization. Resolution is dependent upon the number of photoreceptors, or rhabdomeric cells per eye. The higher the density of cells the finer the resolution of an image (Land 1985). The number of nerve axons exiting a

spider's eye is in a 1:1 ratio with the number of photoreceptors (Uehara & Uehara 1996).

Focal length.—The focal length of each lens was determined using the 'hanging drop' method described in Homann (1928) and Land (1985). The lens, along with a small proportion of the surrounding cuticle, was dissected from the head and stored in spider saline. After being cleared of excess tissue in warm, dilute sodium hydroxide, the lens was suspended in a drop of spider saline from the underside of a cover slip. Using a microscope, the image through the lens was then viewed, targeting an object of known size (o). The distance between the lens and the object was then measured using callipers (μ). The size of the image (i) was determined, and the focal length was calculated, using the formula described by Opell & Ware (1987: Table 1). For each lens type an average of the values measured was determined. Repeated measures ANOVA, with one within subject factor (eye) and no between subject factors, with a Tukey/Kramer post-hoc test, was used to determine differences between the focal lengths of the different eyes.

Sensitivity.—Sensitivity (*f*-number), or the eye's ability to admit light, was calculated using values for focal length (F) and the diameter of the retina (d), measured from the extremities of the rhabdomeres in each species (Opell & Ware 1987). The resulting *f*-number is inversely related to the eyes ability to admit light (Land 1985). Focal lengths were determined by the above methods and retinal diameters were determined by taking measurements from slides obtained using methods described for internal ocular organization. These values were then entered into the sensitivity equation outlined in Opell & Ware (1987: Table 1).

Field of view.—Histological investigation revealed *B. insignis* has a 'canoe shaped' tapetum, which reflects light at an acute angle making it impossible to determine the field of view using ophthalmoscopy (Land 1985). Therefore, the visual field was determined using physical measurements of the lens and the surrounding retinal hemisphere. To determine the field of view, the size and orientation of the visual angle were determined according to methods comparable to those used on uloborids by Opell & Cushing (1986) and Opell & Ware (1987). Two deviations from these methods were employed. Measurements from frontal sections rather than sagittal sections were used and the tapetal periphery was taken to represent the limits of the visual cells and therefore define the width of the retina.

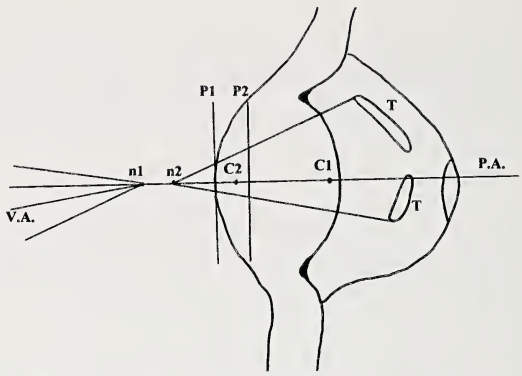


Figure 2.—Diagrammatic section of the secondary eye of B.insignis. n1 = front nodal point; n2 = rear nodal point; C1 = center of curvature of front of lens; C2 = center of curvature of the rear of lens; P1 = front principal plane; P2 = rear principal plane; P.A. = principal axis; T = tapetum; V.A. = visual axis.

Size of visual angle.—To ascertain the field of view of each eye, the angle at which light can enter to activate visual cells must be calculated; this is the visual angle. The visual angle of *B. insignis* was determined mathematically using measurements taken from sections of the eye (Fig. 2). A simple lens has two centers and two radii of curvature, one for both the front surface and the rear surface of the lens. The line joining the two centers is the principal axis of the lens. The refractive index of each lens was required to calculate the front and rear principal planes (Fig. 2), and was determined using measured focal length in conjunction with the radii of curvature of each lens (Table 1). This index was then used to calculate the principal planes (Table 1). The refractive index of air was assumed to be 1.00 and the refractive index of spider saline was assumed to be 1.33 (Land 1969). Drawings were made of each lens and its retinal hemisphere with the principal axis, principal planes and nodal points added to the reconstruction (Fig. 2). The rear nodal point was calculated by measuring the focal length forward from the retinal hemisphere along the principal axis. The front nodal point was then calculated since the distance between the front and

rear nodal points along the principal axis equates to the distance between the principal planes.

To determine the visual angle of each eye, sections from the frontal plane were used. Lines were drawn from the peripheral retinal cells in front of the tapetum to the rear nodal point and the angle these lines made with the principal axis was measured. An inverted projection of this angle from the front nodal point produced the eye's visual field (Fig. 2). A line bisecting this field represents the visual axis. To plot the visual field around the visual axis, the angle made with the principal axis was measured.

Orientation of visual angle.—To accurately plot visual fields, the relative positions of each eye must be known, therefore the principal axis must be determined relative to both its frontal and sagittal planes. The former was determined by placing the specimen under a dissecting microscope attached to a digital camera. A line was drawn to bisect the specimen along the midline. A second line was drawn along the points where the lens merged with the spider's carapace, through the widest part of the eye's ellipse. A third line was then drawn through the center of the eye and perpendicular to the second line drawn. The angle this line made with the midline of the carapace was recorded, and represented the eye's frontal orientation relative to the sagittal plane. To determine the eye's sagittal orientation, a similar method to above was employed in which the spider was placed on its side and a similar set of angles was created to measure the angle of the principal axis relative to the frontal plane.

Total visual arc, the angle of the principal plane and the visual angle were used to plot fields of view for *B. insignis* by moving the principal axis relative to the center of a geological stereonet accounting for the deviations from the sagittal and frontal planes. Visual fields were produced using the visual axis as a central point, around which the angle of the visual arc was plotted.

Uniformity of refractive index.—The refractive index of each lens was required to calculate the size of the visual angle. The methods used in this study to evaluate refractive index in *B. insignis* require that at least two specimens be used; one to determine the eye's focal length and one to determine the lens's physical properties. To reduce error that may result from using two specimens, mean measurements of focal length for each eye type were used, thereby accounting for possible differences in focal lengths between the two specimens.

Representative specimens from the study population have been deposited in the Western Australian Museum. Slide preparations are held in the Zoology Building, School of Animal Biology, University of Western Australia.

RESULTS

External ocular organization.—The eyes of *B. insignis* were widely spaced along the carapace but not deeply set (TEW = 36.69 ± 0.61, TED = 13.06 ± 0.42, n = 20). Diameters of the eyes are shown in Table 2. There was a significant difference in the sizes of the four different types of eyes for *B. insignis* ($F_{19,3}$ = 15.0, $P < 0.001$). The PL eyes were significantly larger than all others, while both pairs of anterior eyes and both pairs of medial eyes were similar in size.

Internal ocular organization.—The AM eyes (Fig. 3) display a typical bi-convex lens formed by a visible thickening of the cuticular layer. The lens is separated from the retina by a layer of columnar vitreous cells. The retina is composed of visual cells and pigment cells. The most anterior portion of the visual cell, which contains the rhabdomeres, borders the vitreous layer and the nuclei lie below.

In the secondary eyes the boundary separating the rhabdomeres from the visual cells is marked by the tapetum. In *B. insignis*, a 'canoe-shape' tapetum, characteristic of most species in the amaurobioid clade (Homann 1971; Land 1985) was found (Fig. 4). The visual cells in these eyes bend around the tapetum, exiting through the opening between the adjacent tapetal plates. In the eyes of *B. insignis*, one discrete nerve bundle was found to emerge from each eye.

Resolution.—The optic nerves from all four pairs of eyes of *B. insignis* were found grouped together, surrounded by muscle along the midline of the prosoma. Identification of the eye from which each of the six nerve bundles originated, was possible by observing the arrival sequence (within the slides) of each nerve bundle and the direction from which it originated. The number of nerve axons (indicating resolution; Table 2) found in *B. insignis*

Table 1.—Equations used in histological methods.

Focal length (F): $F = \frac{i}{o}u$	i image length o object length u object and eye separation F focal length
Refractive index (n): $\frac{1}{F} = (n - 1)\left[\frac{1}{r_1} + \frac{1}{r_2} - \frac{d(n-1)}{nr_1r_2}\right]$	n refractive index r_1 radius of outer curvature r_2 radius of inner curvature d lens thickness
Power of lens surface (P): Front: $P_1 = \frac{\Delta n}{r_1}$ Rear: $P_2 = \frac{\Delta n}{r_2}$	Δn the difference in the refractive index of the front lens and air or the rear lens and the bodily fluids r_1 radius of outer curvature r_2 radius of inner curvature
Equivalent power (P_E): $P_E = P_1 + P_2 - \frac{d}{n}P_1P_2$	P_1 front surface power P_2 rear surface power d lens thickness n refractive index
Principal planes (VH): Front: $V_1H_1 = \frac{d}{n} \times \frac{P_2}{P_E}$ Rear: $V_2H_2 = \frac{d}{n} \times \frac{P_1}{P_E}$	d lens thickness n refractive index P_1 front surface power P_2 rear surface power P_E equivalent power
Nodal points (N): Determined by plotting f-number (sensitivity): $f = \frac{F}{d}$	N_1 front nodal point N_2 rear nodal point F focal length d pigment ring diameter

Figures 3–4.—3. Primary eye of *B. insignis*; 4. Secondary eye of *B. insignis*.

Table 2.—Summary of parameters measured for eyes of *B. insignis*. Values shown are mean values ± standard error (where calculated). Values for resolution are the mean of the left and right eye.

Eye	Eye diameters (as % of carapace) $n = 20$	Resolution (# nerve axons) $n = 1$	Resolution (# nerve axons/ visual angle) $n = 1$	Focal Length (μm) $n = 2$	Sensitivity (1/*f*-number) $n = 1$
AM	4.78 ± 0.15	328	3.5	233.60 ± 17.74	0.86
AL	4.99 ± 0.16	96	3.1	209.26 ± 2.58	0.37
PM	4.31 ± 0.14	119	3.2	210.26 ± 7.68	0.46
PL	5.71 ± 0.21	102	4.3	198.06 ± 4.38	0.34

was greatest for the AM eyes, followed in order by the PL, PM, and AL eyes. To compare the density of visual cells the number of nerve axons was divided by the size of the visual angle. All eyes were similar in density, being slightly greater in the PL, followed in order by the AM, PM and AL eyes (Table 2). This suggests that the retinal cell number in the AM eyes only maintains the resolution of these eyes, given their larger visual angle, and does not increase their resolution.

Focal length.—The eyes of *B. insignis* displayed no significant differences in focal length ($F_{1,3} = 3.1$, $P = 0.191$; Table 2).

Sensitivity.—Calculated *f*-numbers for *B. insignis* were relatively high (demonstrating a low amount of sensitivity; Table 2). The highest sensitivity in *B. insignis* was found in the AM eyes, which showed a considerably lower *f*-number than all other eyes in this species. The remaining AL, PL, and PM eyes had similar low sensitivities (Table 2).

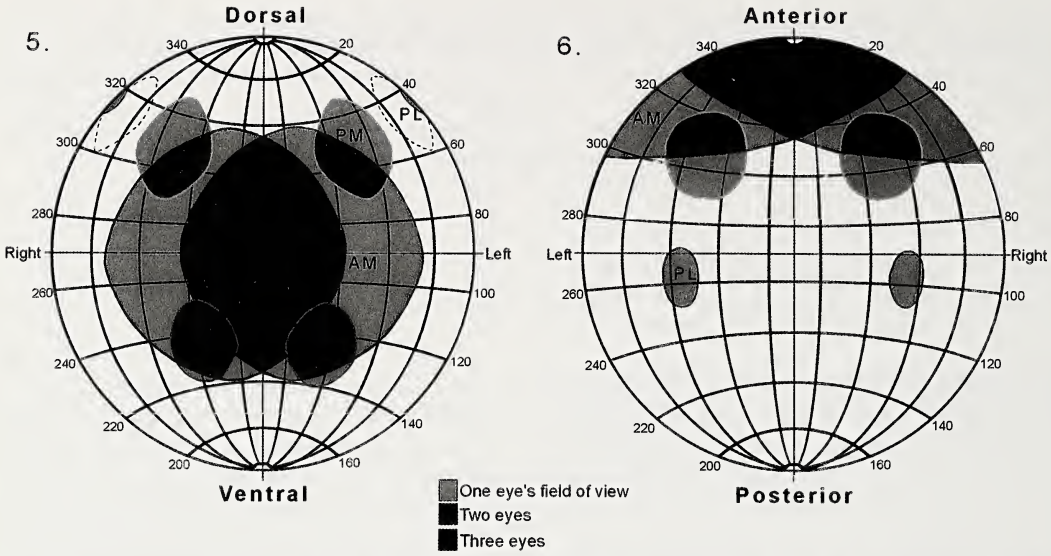
Field of view.—Table 3 provides values used to calculate the field of view for *B. insignis*. The AM eyes showed the greatest field of view, covering 130° along the horizontal meridian (Figs. 5 & 6). They also had a large degree of forward facing overlap, extending 55° above and below the horizontal, and having a maximum overlap of 66° on the horizontal meridian. Both sets of posterior eyes and the AL eyes have small visual fields (less than 40° horizontally or vertically) that show no overlap (Figs. 5 & 6). Both pairs of posterior eyes are directed 50° above horizontal, with the PM eyes directed anteriorly and the PL eyes laterally.

DISCUSSION

Badumna insignis has two rows of four eyes, reminiscent of a primitive external organization (Homann 1971), with all eyes showing little histological differentiation, or differences in diameter, resolution or focal length. The AM eyes were the most specialized, with the greatest sensitivity, the largest field of view and were the only eyes to display binocular overlap. None of the eyes of *B. insignis* displayed the long distance vision or resolution used for detecting prey at a distance.

However, there is a tradeoff between resolution and sensitivity due to physical restrictions of eye size (Blest & Land 1977). The visual system of *B. insignis* seems to be selected for sensitivity rather than resolution, as the resolution is low, even for web-building spiders. The orb weaver *Argiope amoena* (L. Koch 1878) typically has 400–500 optical nerve axons exiting the AM eyes (Uehara et al. 1977), which is greater than the resolution found in *B. insignis*.

The sensitivity of the secondary eyes in *B. insignis* (2.16–2.97) is far less than that of the nocturnally active web building uloborids, whose *f*-number ranges from 0.88–1.70 (Opell & Ware 1987). Instead, they more closely reflect those of the visually hunting diurnal jumping spiders, which have *f*-numbers ranging from 2.68–5.90 (Foelix 1982; Land 1969). This suggests that *B. insignis* utilize their secondary eyes under higher light levels. *Badumna insignis* is occasionally active during the day (Henderson & Elgar 1999) thus, the secondary eyes may be utilized during these periods. Conversely the *f*-number of the AM eyes of *B. insignis* resembles that of the nocturnal uloborids and appears more suitable for its typical nocturnal habit. This combination of sensitivities may allow *B. insignis* to be a more versatile hunter, predominately active in low light-levels, but capable of taking advantage of occasional daylight opportunities.



Figures 5–6.—Fields of view for *B. insignis*: 5. Anterior view; 6. Dorsal view. AM = anterior median eyes; AL = anterior lateral eyes; PM = posterior median eyes; PL = posterior lateral.

However, the lack of binocular vision displayed by any of the secondary eyes would restrict depth perception and therefore limit the use of these eyes in prey capture. The possible function of the secondary eyes remains unclear. With such small fields of view it is unlikely they would be useful in prey detection. These secondary eyes may be used for distinguishing light levels to control circadian rhythms (Uehara et al. 1994), or act simply as wide angle detectors of movement. Conversely, the AM eyes with their large forward facing fields of view and large area of binocular vision, would play an important role in recognition and judgement of distance to the entangled prey.

The web increases the perceptive area of a spider (Peters & Pfreundt 1986) and evidence suggests spiders can determine the identity of an object in the web by the vibrations it creates (Suter 1978; Barth 1982; Masters et al. 1986; Herberstein *et al.* 1998). Coupled with its poor visual acuity, this suggests that *B. insignis* relies on its web rather than its eyes for prey detection. The web of *B. insignis* also acts to entangle and ensnare prey, and so also plays a significant role in prey capture.

The relatively unspecialized visual system

Table 3.—Ocular properties and measurements used to calculate and plot fields of view for *Badumna insignis*.

Eye	Lens thickness (μm)	Radius of curvature (r1/r2, μm)	Refractive index	Pigment ring diameter (μm)	*f*-number	Total visual angle	Visual axis from physical axis	Visual axis from frontal plane	Visual axis from sagittal plane
AM	184.7	142.7/107.8	1.31	200.8	1.16	93°	8° right of right eye	0°	9°
AL	129.0	126.9/108.2	1.32	87.4	2.67	32°	6° right of right eye	33° ventral	20°
PM	109.4	108.3/98.5	1.28	97.5	2.16	37°	19° right of right eye	38° dorsal	33°
PL	91.5	112.3/97.8	1.29	33.3	2.97	24°	1° right of right eye	44° dorsal	90°

of *B. insignis* may be attributed to the utilization of the web. As well as functioning to ensnare prey, a web can also be protective. A complete field of view is not essential as the web warns the spider of some potential threats and provides a hidden retreat. The web essentially functions to increase the perceptive area for prey capture and may act in place of a highly developed visual system. However, *B. insignis* still requires a system for recognizing whether an object within the web is predator or prey. The araneophagic spider *Lampona cylindrata* (L. Koch 1866) (Araneae Lamponidae) is commonly known to prey upon *Badumna insignis* (Hickman 1967; Main, pers obs). The eyes of *B. insignis* appear adapted for close range recognition, due to the short-range focus and good depth perception of the AM eyes. Thus the visual system operates to inform *B. insignis* of the distance to an object and whether to attack or retreat.

ACKNOWLEDGEMENTS

We are grateful to the following people from the School of Animal Biology, University of Western Australia: Professor Lyn Beazley, for specialist information on optic nerves; Wally Gibb, for advice on collection of specimens; Phil Runham, for help with experimental methods and general advice. We would also like to thank the reviewers for their time and helpful comments on this manuscript.

LITERATURE CITED

Barth, F.G. 1982. Spiders and vibratory signals: sensory reception and behavioural significance. Pp. 67–122. *In* Spider Communication: Mechanisms and Ecological Significance (P.N. Witt & J.S Rovner, eds.). Princeton University Press, Princeton, New Jersey.

Blest, A.D. & M.F. Land. 1977. The physiological optics of *Dinopis subrufus* (L. Koch): a fish-lens in a spider. Proceedings of the Royal Society of London B. Biological Sciences 196:197–222.

Comstock, J.H. 1948. The Spider Book. Comstock Publishing Company Inc., New York.

Dacke, M., T.A. Doan & D.C. O'Carroll. 2001. Polarized light detection in spiders. Journal of Experimental Biology 204:2481–2490.

Foelix, R.F. 1982. Biology of Spiders. Harvard University Press, Cambridge.

Forster, L.M. 1979. Visual mechanisms of hunting behaviour in *Trite planiceps*, a jumping Spider (Araneae: Salticidae). New Zealand Journal of Zoology 6:79–93.

Grusch, M., F.G. Barth, & E. Eguchi. 1997. Fine structural correlates of sensitivity in the eyes of the ctenid spider, *Cupiennius salei* Keys. Tissue & Cell 29:421–430.

Harland, D.P. & R.R. Jackson. 2000. Cues by which *Portia fimbriata*, an araneophagic jumping spider, distinguishes jumping-spider prey from other prey. Journal of Experimental Biology 203: 3485–3494.

Harland, D.P. & R.R. Jackson. 2002. Influence of cues from the anterior medial eyes of virtual prey on *Portia fimbriata*, an araneophagic jumping spider. Journal of Experimental Biology 205: 1861–1868.

Henderson, R.J. & M.A. Elgar. 1999. Foraging behaviour and the risk of predation in the black house spider, *Badumna insignis* (Desidae). Australian Journal of Zoology 47:29–35.

Herberstein, M.E., K.E. Abernethy, K. Backhouse, H. Bradford, F.E. de Crespigny, P.R. Luckock & M.A. Elgar. 1998. The effect of feeding history on prey capture behaviour in the Orb-Web spider *Argipoe keyserlingi* Karsh (Araneae: Araneidae). Ethology 104:565–571.

Hickman, V.V. 1967. Some common spiders of Tasmania. Tasmanian Museum and Art Gallery, Hobart.

Homann, H. 1928. Bietrage zur Physiologie der Spinnenaugen. I. Untersuchungsmethoden. II. Das Sehvermogen. Zeitschrift Fuer Vergleichende Physiologie 7:201.

Homann, H. 1971. The eyes of Araneae. Zeitschrift Fur Morphologie Der Tiere 69:201–272.

Kovoor, J., A. Munoz-Cuevas & J. Ortega Escobar. 1992. The visual system of *Lycosa-tarentula-fasciiventris* Araneae Lycosidae I. Organization of optic nerves and first ganglia. Annales des Sciences Naturelles-Zoologie et Biologie Animale 13:25–36.

Land, M.F. 1969. Structure of the retinae of the principal eyes of jumping spiders (Salticidae: Dendryphantinae) in relation to visual optics. Journal of Experimental Biology 51:443–470.

Land, M.F. 1985. The morphology and optics of spider eyes. In Neurobiology of Arachnids. (F.G. Barth, ed.). Springer-Verlag, New York.

Land, M.F. & F.G. Barth. 1992. The quality of vision in the ctenid spider *Cupiennius salei*. Journal of Experimental Biology 164:227–242.

Lizotte, R.S. & J.S. Rovner. 1988. Nocturnal capture of fireflies by lycosid spiders: visual versus vibratory stimuli. Animal Behaviour 36:1809–1815.

Main, B.Y. 1964. Spiders of Australia. Axiom Books, Australia.

Main, B.Y. 1976. Spiders. Collins Publishing, Sydney.

Main, B.Y. (2001). Historical ecology, resposes to current ecological changes and conservation of

Australian spiders. Journal of Insect Conservation 5:9–25.

Masters, W.H., H.S. Markl & A.J.M Moffat. 1986. Transmission of vibration in a spider's web. Pp. 49–69. *In* Spiders: Webs, Behaviour and Evolution. (W.A. Shear, ed.). Stanford University Press, Stanford.

Opell, B.D. 1988. Ocular changes accompanying eye loss in the spider family Uloboridae. Journal of Morphology 196:119–126.

Opell, B.D. 1999. Changes in the spinning anatomy and thread stickness associated with the origin of orb-weaving spiders. Biological Journal of the Linnean Society 68:583–612.

Opell, B.D. & P.E. Cushing. 1986. Visual fields of the orb web and single line web spiders of the family Uloboridae (Arachnida, Araneida). Zoomorphology 106:199–204.

Opell, B.D. & A.D. Ware. 1987. Changes in visual fields associated with web reduction in the spider family Uloboridae. Journal of Morphology 192: 87–100.

Ortega-Escobar, J. & A. Munoz-Cuevas. 1999. Anterior median eyes of *Lycosa tarentula* (Araneae, Lycosidae) detect polarized light: Behavioural experiments and electroretinographic analysis. Journal of Arachnology 27:663–671.

Parker, A.R. & Z. Hegedus. 2003. Diffractive optics in spiders. Journal of Optics A—Pure and Applied Optics 5:S111–S116.

Persons, M.H & G.W. Uetz. 1996. The influence of sensory information on patch residence time in wolf spiders (Araneae, Lycosidae). Animal Behaviour 51:1285–1293.

Persons, M.H & G.W. Uetz. 1998. Presampling sensory information and prey density assessment by wolf spiders (Araneae, Lycosidae). Behavioural Ecology 9:360–366.

Peters, W. & C. Pfreundt. 1986. The distribution of trichibothria and lyriform organs on the legs of spiders with different habits. Zoologische Beitraege 29:209–226.

Rovner, J.S. 1993. Visually mediated responses in the Lycosid spider *Rabidosa rabida*: the roles of different pairs of eyes. Memoirs of the Queensland Museum 33:635–638.

Schmid, A. 1998. Different functions of different eye types in the spider *Cupiennius salei*. Journal of Experimental Biology 201:221–225.

Suter, R.B. 1978. *Cyclose turbinata* (Araneae: Araneidae): Prey discrimination via web-bourne vibrations. Behavioural Ecology and Sociobiology 3:283–296.

Uehara, A. & K. Uehara. 1996. Efferent fibers and the posteromedial eye of the liphistiid spider *Heptathela kimurai* (Araneae: Liphistiomorphae). Journal of Experimental Zoology 275: 331–338.

Uehara, A., K. Uehara & K. Ogawa. 1994. Fine structure of the anteromedial eye of the liphistiid spider *Heptathela kimurai*. Anatomical Records 240:141–147.

Uehara, A., T. Toh & H. Tateda. 1977. Fine structure of the eyes of orb-weavers, *Argiope amoena* L. Koch (Araneae: Argiopidae). 1. The antermedial eyes. Cell Tissue Research 182:81–91.

Zwicky, K.T. 1968. Innervation and pharmacology of the heart of *Urodacus*, a scorpion. Comparative Biochemistry and Physiology 24:799–808.

Manuscript received 10 June 2004, revised 28 November 2004.

2005. The Journal of Arachnology 33:735–744

A NEW SPECIES OF *BOTHRIURUS* FROM BRAZIL (SCORPIONES, BOTHRIURIDAE)

Camilo Iván Mattoni[1] and **Luis Eduardo Acosta**: Cátedra de Diversidad Animal I, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Av. Vélez Sarsfield 299, X5000JJC Córdoba, Argentina. E-mail: cmattoni@com.uncor.edu

ABSTRACT. A new species of scorpion from southern Brazil, *Bothriurus pora*, is described. The hemispermatophore of this species is unique within the genus, displaying a highly developed and extremely complex capsular region. External morphology and shape of the sperm packages show a close relationship with the *Bothriurus bonariensis* species group.

RESUMEN. Se describe una nueva especie de escorpión del sur del Brazil, *Bothriurus pora*. El hemiespermatóforo de esta especie presenta caracteres únicos en el género, con una región capsular muy desarrollada y extremadamente compleja. Su morfología externa y la forma general de sus paquetes espermáticos demuestran una relación cercana con el grupo de especies *Bothriurus bonariensis*.

Keywords: Scorpiones, Bothriuridae, *Bothriurus*, bonariensis group, taxonomy, Brazil, Neotropics

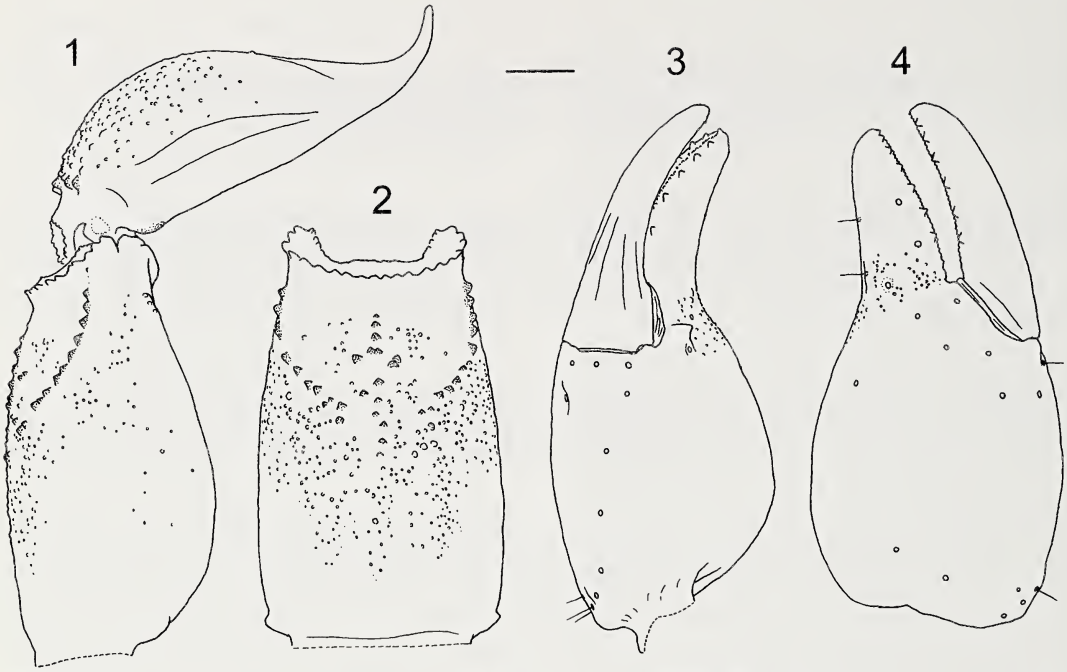
The genus *Bothriurus* Peters 1861 (Scorpiones, Bothriuridae) comprises small to medium-sized scorpions, distributed over a large part of South America (Argentina, Chile, Uruguay, Bolivia, Paraguay, southern Peru, and from southern to northwestern Brazil) in diverse habitats including deserts, steppes, dry forests, mountains, savannas and rainforests (Maury 1979, 1982; Lourenço & Maury 1979; Acosta & Ochoa 2002; Mattoni 2003). The genus currently contains 36 valid nominal species (Lowe & Fet 2000; Mattoni 2002a, 2002b, 2002c; Ojanguren Affilastro 2002, 2003), although the actual number should reach around 45 (Mattoni 2003), making it the most diverse genus of Bothriuridae. *Bothriurus* species are presently placed in 13 species groups, characterized by both somatic and genitalic characters (Maury 1979, 1982, 1984; Lourenço & Maury 1979; Maury & Acosta 1993; Mattoni 2002b). These "groups" show considerable internal uniformity, and some may be monophyletic (Acosta & Peretti 1998; Mattoni 2003). Although a previous analysis (Prendini 2000, 2003) questioned the monophyly of *Bothriurus*, a more recent phylogenetic analysis demonstrates, albeit with weak support, that *Bothriurus* is monophyletic (Mattoni 2003).

During the course of a larger revision of *Bothriurus*, a single *Bothriurus* male that could not be assigned to any of the known species groups, was discovered in the collection of the Instituto Butantan, São Paolo, Brazil. Its external morphology suggested a close relationship to the *bonariensis* group (Maury & Acosta 1993; Ojanguren Affilastro 2003), but the complex morphology of its hemispermatophore was unlike any other species of *Bothriurus*. The specimen is described below as *B. pora* new species.

METHODS

Terminology for general morphology follows that of Stahnke (1970), except for the pedipalp (Francke 1977) and metasomal carinae (Prendini 2000, 2003), trichobothrial nomenclature (Vachon 1974) and pedipalp segmentation (Sissom 1990). The nomenclature of the hemispermatophore is based on San Martín (1963, 1965), Peretti (1992) and Maury & Acosta (1993); we maintained the abbreviations derived from the names in Spanish, since they were widely used in the literature. Carinae of metasomal segments are

[1] Current address: Department of Invertebrate Zoology, American Museum of Natural History, 79th St. at Central Park West, New York, NY 10024 USA. E-mail: emattoni@amnh.org



Figures 1–4.—*Bothriurus pora* new species, holotype male (IBSP–SC); 1. Metasomal segment V and telson, lateral view; 2. Metasomal segment V, ventral view; 3–4. Right pedipalp chela; 3. Ventrointernal view; 4. External view. Scale bar = 1 mm.

abbreviated as follows: Dsm = dorsal submedian; Dl = dorsal lateral; Lsm = lateral supramedian; Lm = lateral median; Li = lateral inframedian; Vl = ventral lateral; Vsm = ventral submedian; Vm = ventral median. Hemispermatophore structures: L = lamina; c.d. = distal crest of lamina; r.f. = frontal fold; c.f. = frontal crest; P.b. = basal portion; l.i. = internal lobe of capsule; l.b. = basal lobe of capsule; l.e. = external lobe of capsule; c.c. = capsular concavity; r.b. = basal fold. The material examined are deposited at Instituto Butantan, São Paulo, Brazil (IBSP-SC); Cátedra de Diversidad Animal I, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Argentina (CDA); Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil (MCN); and Museu de Zoologia da Universidade de São Paulo, Brazil (MZUSP). All measurements are in mm and were taken using an ocular micrometer. Illustrations were produced using a Leica MS5 stereomicroscope and camera lucida.

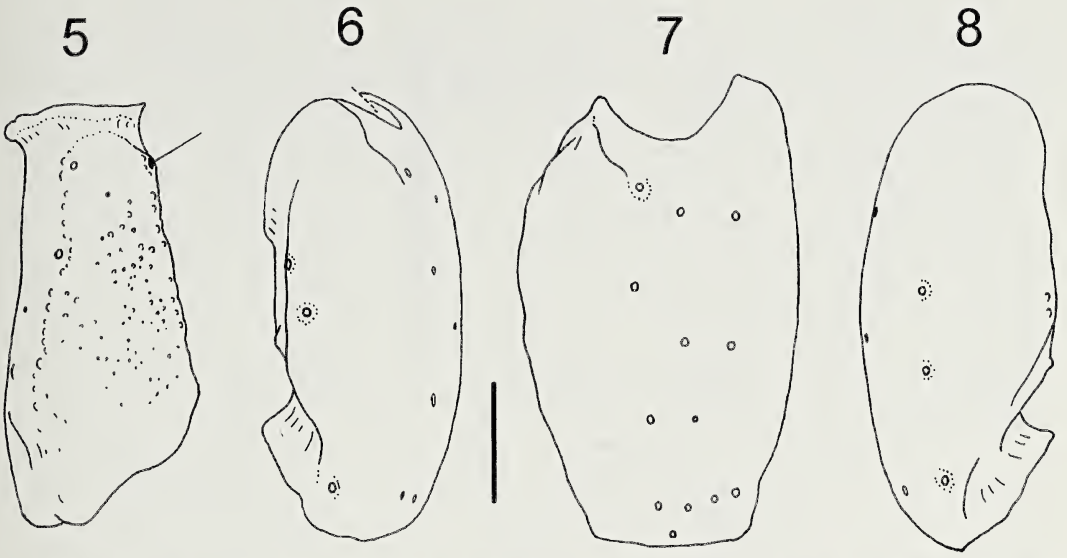
Bothriurus pora new species
Figs. 1–16, 23

? *Bothriurus bonariensis*: Brazuna & Koller, 1998: 1 (probable misidentification).

Type.—Holotype male, BRAZIL: *Estado de Mato Grosso do Sul*: Ponta Porã (22°32′S, 55°43′W), 652 m, 13 December 1966, N.P.V. Salvaeno (IBSP-SC 937).

Etymology.—The species name is a noun in apposition taken from the type localiy.

Diagnosis.—In terms of external morphology, *B. pora* appears most closely related to the bonariensis group: *B. bonariensis* (C.L. Koch 1842), *B. chacoensis* Maury & Acosta 1993, and *B. jesuita* Ojanguren Affilastro 2003. All of these species share a similar arrangement of the ventral carinae of metasomal segment V. However, subtle differences exist. In *B. bonariensis*, the Vl and Vsm carinae are almost connected medially (Figs. 19, 20), whereas in the other species they are not completely fused, leaving a small median gap; the most distal granules of the Vm carina (slightly more developed) are placed in that space. The ventral surface of segment V is noticeably granular in *B. pora* (Fig. 2), compared with other species of the bonariensis group, in which it is smooth (Fig. 20). The Dsm carinae of the metasomal segments I to IV are more weakly developed in the bonariensis group (represented only by terminal granules),



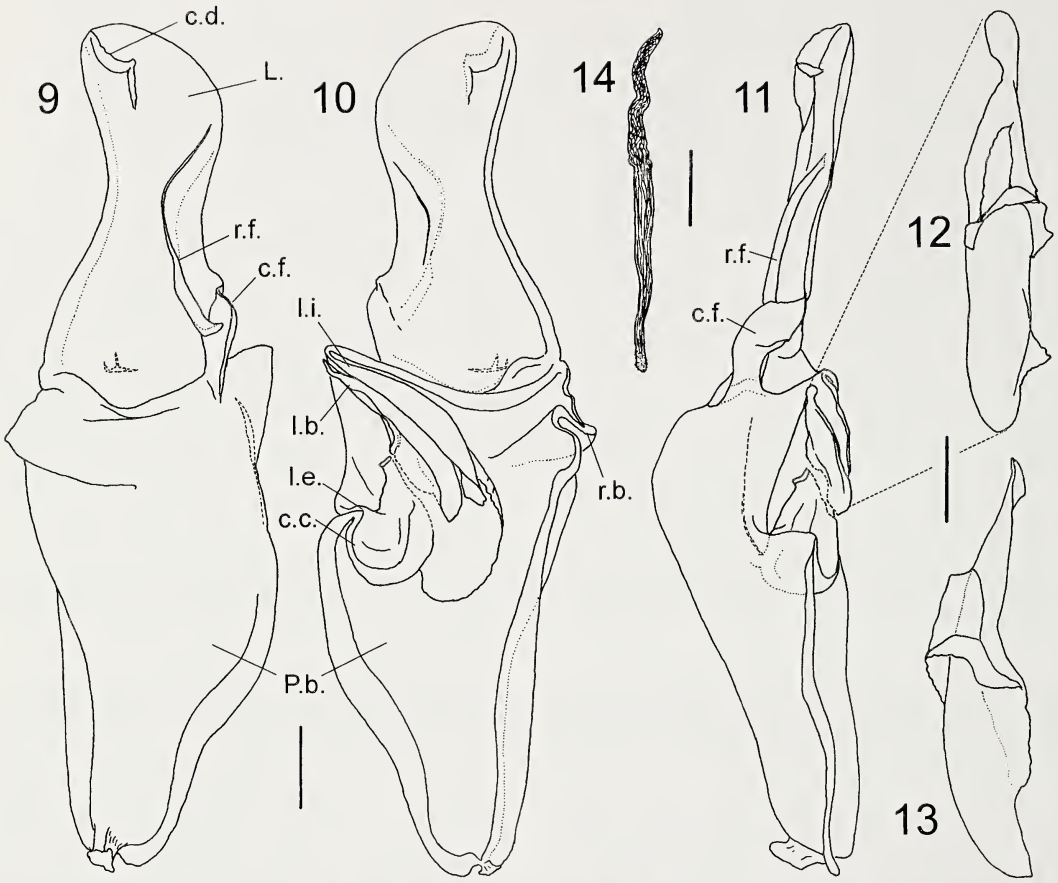
Figures 5–8.—*Bothriurus pora* new species, holotype male (IBSP–SC); 5. Right pedipalp femur, dorsal view; 6–8. Right pedipalp patella; 6. Dorsal view; 7. External view; 8. Ventral view. Scale bar = 1 mm.

whereas in *B. pora* they are granular throughout. *Bothriurus pora* shares with the bonariensis group a robust habitus and dark coloration. Another important similarity is the pronounced dorsal gland of the male telson, which occupies the entire dorsal surface of the vesicle. However, in the bonariensis group, the gland is contained in a large depression which is absent in *B. pora*. The chaetotaxy of the metasoma is quite similar between the species of the bonariensis group and *B. pora* (Figs. 15–18), however, the latter shows a pair of ventromedian chetae on Segment III that is absent in the bonariensis group.

In spite of many external similarities, the hemispermatophore of *B. pora* is markedly different. The hemispermatophore of *B. pora* is unique in *Bothriurus*, presenting characters not previously observed in other bothriurid species (Figs. 9–13). The lamina exhibits a well developed r.f. and c.f., and a curved internal crest. The lobe region is extremely complex, with l.b. elongated and concave, bearing partitions in its dorsal surface. In the bonariensis group, the lamina is more elongated, with c.f. much more extended, and l.b. larger and triangular in shape (Figs. 21, 22). A feature shared by both *B. pora* and the *B. bonariensis* species group is the general morphology of the sperm packages (as preserved in 80% ethanol), which display a strongly gnarled, helicoidal anterior region (Peretti & Battán-Horenstein 2003). In *B. pora*, however, the degree of torsion is less marked than in the *bonariensis* group.

Several robust synapomorphies (e.g., shape and size of spiracles, shape of sperm packages, position of *Et3* trichobothria on chela) suggest that *B. pora* is the sister taxon of the *bonariensis* species group (Mattoni 2003). Also the bonariensis species group is supported by several synapomorphies: the large depression on the dorsal surface of the telson, the hemispermatophore (similar in all the species of the group), and the pigmentation pattern of the ventral face of the metasoma (with two lateral stripes) (Mattoni 2003). However, the hemispermatophore of *B. pora* is clearly divergent, with many unique charactes not previously observed in the family Bothriuridae (see, e.g., Maury 1980). The structure of the basal lobe, which bears thin dorsal walls, raises questions about its function, as this part enters the female atrium during sperm transfer (Peretti 1992).

The helicoidal end of the sperm package in *B. pora* and the three species of the bonariensis group, has not been recorded in other *Bothriurus* species, or in any other bothriurid (Peretti & Battán-Horenstein 2003; Mattoni 2003). The shape observed in *B. pora*, with a slightly helicoidal end, might represent an intermediate condition between the marked helicoid in the bonariensis group and the straight

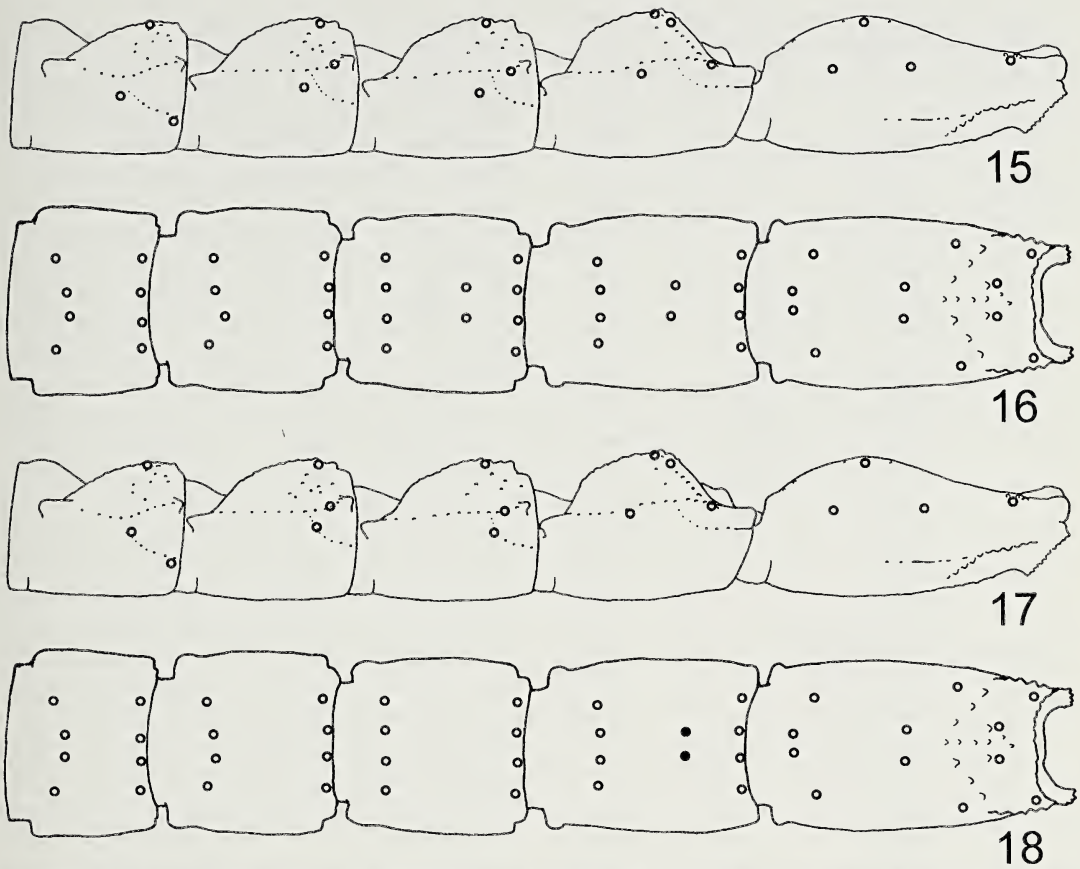


Figures 9–14.—*Bothriurus pora* new species, holotype male (IBSP–SC); 9–13. Right hemispermatophore; 9. External view; 10. Internal view; 11. Frontal view; 12–13. Detail of basal lobe; 12. Dorsal view; 13. Laterointernal view; 14. Sperm package. Scale bars = 1 mm (Figs. 9–11); 0.5 mm (Figs. 12–13); 50 μm (Fig. 14).

condition of all remaining *Bothriurus* species (Mattoni 2003). Similarly, the morphology of the front crest (c.f.) of the hemispermatophore in *B. pora* resembles that observed in the bonariensis group, which display a plain front surface and undulated edge, though much less strongly developed.

Since the bonariensis group is longely defined through its characteristic hemispermatophore morphology, we are convinced that is not advisable to include *B. pora* as a member of this group, maintaining it just as its sister taxon.

Description.—*Coloration:* In general, brown to orange-brown, with patches of dark brown pigmentation. Carapace brown, densely pigmented near the median ocelli, and extended laterally; transverse spot on anterior margin, posterolateral margins reticulate. Tergites almost completely and diffusely pigmented, more densely on the pretergites and the posterior edge; submedian areas with small, irregular clear dots inside the pigmented area. Legs yellowish, densely spotted prolaterally and retrolaterally; tarsi depigmented. Coxa, genital operculum and pectines faintly reticulate. Chelicerae yellowish, with very faint spots dorsally, forming longitudinal stripes that reunite transversely at the base of the fingers. Pedipalp patella and femur with numerous spots dorsally; chela with longitudinal stripes externally, joining transversely near the base of the fingers. Sternites broadly pigmented, increasing in intensity from sternite I-V. Metasoma dark orange-brown. Segments I-IV each with a wide diffuse subtriangular spot dorsally, and a transverse spot on the posterior border; segment V with a pale spot of retic-



Figures 15–18.—Distribution of macrosetae on metasoma (carinae schematic, not to scale); 15–16. *Bothriurus pora* new species, holotype male (IBSP–SC); 15. Lateral view; 16. Ventral view. 17–18. *Bothriurus bonariensis* group; 17. Lateral view; 18. Ventral view (the pair of setae in black is absent in *B. bonariensis*).

ulate, diffuse pigment, proximally. Lateral surfaces diffusely reticulate, reticulations merging ventrolaterally. Ventral surface with three longitudinal stripes (median weaker) uniting in distal half or one third of each segment. Telson reddish brown, almost depigmented, but with a narrow, longitudinal, median line ventrally; and a wide yellow area ventrally.

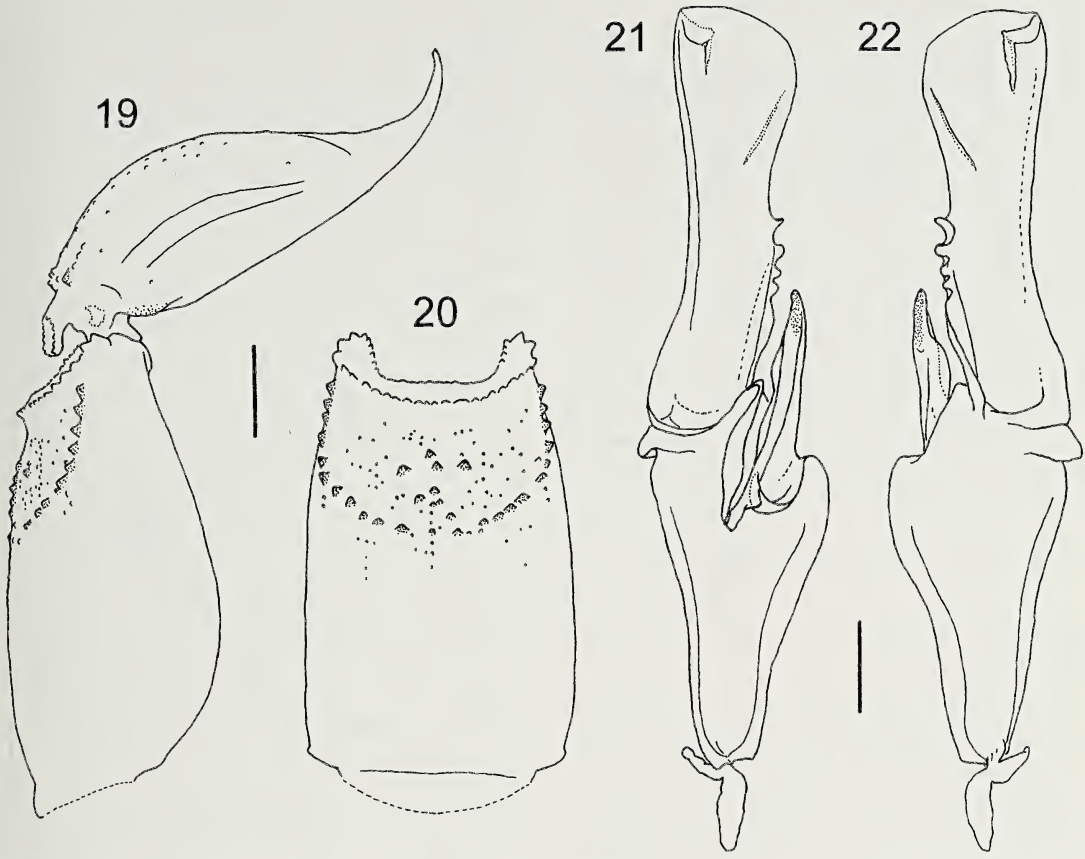
Morphology: Medium-sized scorpion of robust habitus. Total length: 38.11 mm (detailed measurements: Table 1). Carapace and tergites very finely and evenly granular, giving matt appearance. Carapace: three pairs of lateral ocelli; ocular tubercle prominent, median ocelli separated by one diameter; anterior margin with weak median notch, anterior median and anterior marginal furrows only weakly developed; median ocular furrow present, lateral ocular furrows weak, median and posteromedian furrows strong, with a depressed area in between, posterior transverse furrows absent, posterolateral furrows well developed. Tergites I-VI acarinate, VII with four short carinae in the posterior quarter, two submedian and two lateral, with scattered granules in between. Sternites acarinate, smooth; spiracles elongated and narrow. Carinae of metasomal segments I-IV: Dsm entire, formed by low granules, the distal one more strongly developed; Dl present in the posterior half of segments I and IV, and the posterior fifth of segments II and III; surface between Dsm and Dl with scattered granules; Li vestigial in posterior third of segments I and II, absent on III and IV; Vl and Vsm absent. Carinae of metasomal segment V: Dl only present in posterior third, very weak; Lm absent; area between Dl and Vl with small, scattered granules, more abundant in posterior half; Vl

Table 1.—Measurements (mm) of the holotype male of *Bothriurus pora* new species.

Total length		38.11
Carapace	length	5.63
	anterior width	3.34
Mesosoma	length	9.37
Metasoma	length	23.21
	segment I, length	2.27
	width	3.87
	segment II, length	2.73
	width	3.67
	segment III, length	3.07
	width	3.60
	segment IV, length	3.80
	width	3.60
	segment V, length	5.00
	width	3.47
	height	2.93
Telson	length	6.34
	width	2.93
	height	2.07
	aculeus, length	1.67
Pedipalp	total length	14.63
	femur, length	3.54
	width	1.60
	patella, length	3.87
	width	1.73
	chela, length	7.22
	width	2.60
	height	3.74
	movable finger, length	3.87

limited to posterior quarter, and connected with oblique VSM, together forming an open arc; VM present in posterior half, with a pair of accessory submedian granules posteriorly; area posterior to the VL+VSM arc slightly depressed, with small granules; surface anterior to the VL+VSM arc finely granular, granules more abundant posteriorly. Metasomal macrosetae as in Figs. 15 & 16. Telson: vesicle oval, ventral surface granular, with larger granules towards proximal third; dorsal surface smooth and not depressed, with a wide glandular area almost covering the dorsal surface. Chelicerae: one subdistal tooth on movable finger; ventral surface of hand and movable finger covered with abundant, fine setae. Pedipalps. Femur with three carinae comprising blunt granules; dorsointernal carina restricted to proximal half, with sparse granules distally; dorsoexternal carina well developed, becoming obsolete towards distal quarter; ventrointernal carina present in proximal half, weakening distally; dorsal and internal surface with abundant scattered granules, ventral surface with only a few small granules, external surface smooth. Patella with two weak vestigial carinae, dorsointernal and ventrointernal, each represented by only one proximal granule. Chela robust, acarinate, surface almost smooth, with only a few small granules behind base of fixed finger; a strong conical apophysis evident near base of movable finger, internally, slightly curved dorsally, with a slight depression internally. Trichobothrial pattern type C, neobothriotaxic major, with the following segment totals: femur 3 (1 *d*; 1 *i*; 1 *e*), patella 19 (2 *d*; 1 *i*; 13 *e*; 3 *v*) and chela 27 (17 manus, with 5 *V* ; 6 fixed finger); chela: *Esb* near to Eb_2 and Eb_3, Et_3 aligned with *Est.* Sternum slitlike, represented by a narrow transversal plate. Genital operculum loosely joined together along the anterior one-fourth of their length, isosceles triangle shaped, with the more acute angle towards posterior. Number of pectinal teeth: 19–19. Hemispermatophore: heavily sclerotized; L. large and straight, narrowing medially; c.d. strong, divided by a transverse crest (terminally curved, basally straight, parallel to the axis of L.); r.f. well developed on external surface of L., long and curved, enlarging towards base of L.; connecting to a short c.f., which extends from dorsal limit of P.b. to basal quarter of L. (c.f. straight basally and slightly sinuous on the terminal edge; front surface plain); on the interior side of L., a small curved crest is present; P.b. wide, slightly longer than L.; r.b. well developed, sinuous; lobe region large, highly complex, occupying superior half of P.b.; l.b. laminar, elongated and concave, with a spatulate end; on its anterior half, two thin dorsal trabeculae (one transverse, the other longitudinal) present; interior portion of l.i. large; l.e. with well developed c.c. Sperm packages (preserved in 80% ethanol): "head" portion visible by refringence as a darker area on the anterior third of the package, helicoidal in shape; medially corrugated; "tail" straight, becoming acute posteriorly, showing small granulations (some packages stick to each other at this point).

Distribution.—Only known from the type locality, in the southernmost part of the Cerrado Biogeographic Province (SE Brazil). A record of *B. bonariensis* from the urban area of Campo Grande, Mato Grosso do Sul (Brazuna & Koller 1998) is probably referable to



Figures 19–22.—*Bothriurus bonariensis*, male from Toledo, Córdoba (CDA); 19. Metasomal segment V and telson, lateral view; 20. Metasomal segment V, ventral view; 21–22. Left hemispermatophore; 21. Internal view; 22. External view. Scale bars = 1 mm (Figs. 19–20); 0.5 mm (Figs. 21–22).

B. pora. The single known record of *B. pora* is allopatric with respect to the known distribution of the *bonariensis* group, all component species of which are also allopatric with one another (Fig. 23). *Bothriurus bonariensis* inhabits the Pampean Biogeographic Province and a large portion of the "Espinal" Province (as defined by Cabrera & Willink 1980), whereas *B. chacoensis* is almost restricted to the western district of the Chacoan Province (Maury 1973; Maury & Acosta 1993; Acosta & Maury 1998). *Bothriurus jesuita*, the sister species of *B. chacoensis* (Ojanguren-Affilastro 2003; Mattoni 2003), has a very similar hemispermatophore morphology (a filament at the end of the basal lobe of the right hemispermatophore), and occurs in northeast Argentina and southern Brazil (Maury & Acosta 1993; Ojanguren-Affilastro 2003). The type locality of *B. pora* is in the Sierra Amambaí, almost on the southeast border of the state Mato Grosso do Sul (close to the boundary with Paraguay). This locality lies in the Cerrado Biogeographic Province (Cabrera & Willink 1973).

We believe that the material cited by Brazuna & Koller (1998) as *B. bonariensis* from Campo Grande (Mato Grosso do Sul) should be referred to *B. pora* instead, taking into account that Campo Grande is close to Ponta Porã, on the slopes of the Sierra Maracajú (a geographical extension of the Sierra Amambaí). The fairly well known range of *B. bonariensis* is distant from both of these sites (Fig. 23), and the habitats occupied by this species are very different to the Cerrado.

The pattern of allopatric distribution among these four related species is shown by several other *Bothriurus* species groups, e.g., the prospicuus group (Mattoni & Acosta 1997; Acosta & Peretti 1998; Ojanguren Affilastro 2002; Mattoni 2003), the vittatus group (Mat-

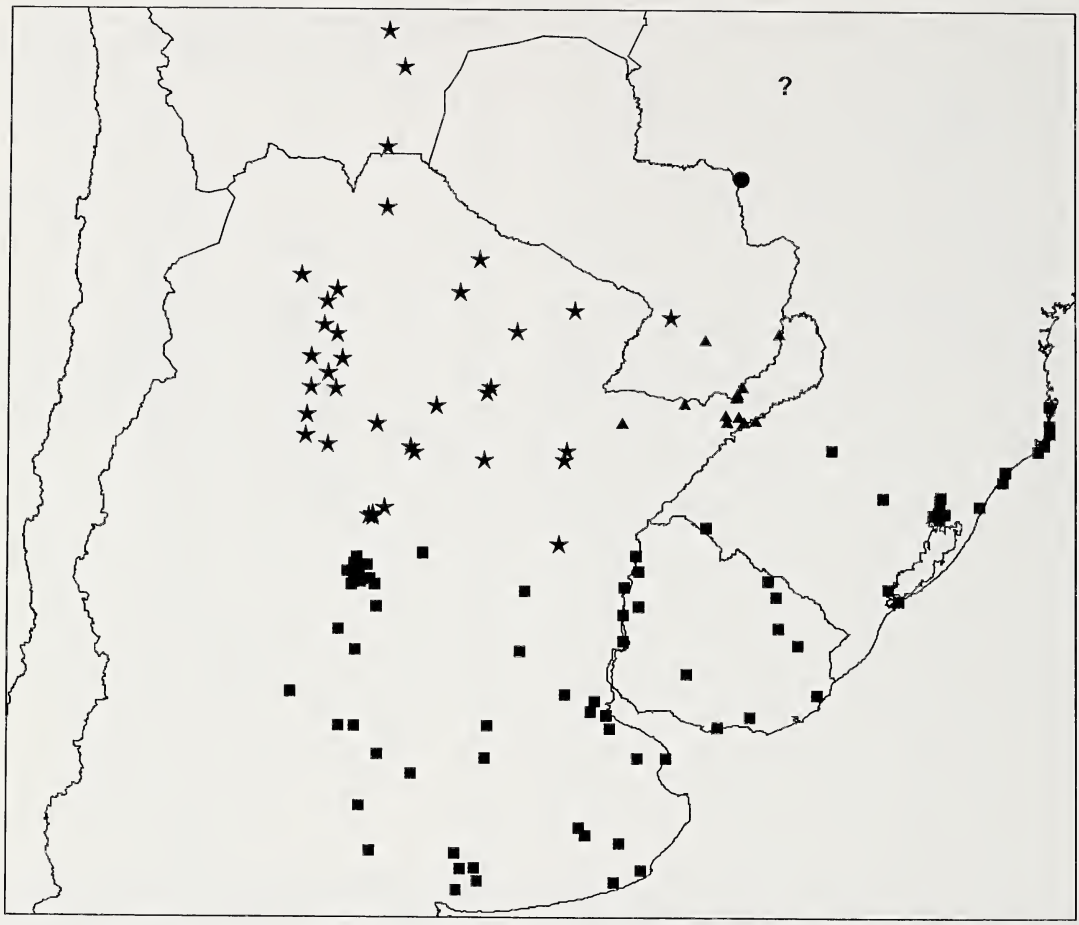


Figure 23.—Distribution map of *Bothriurus pora* new species (type locality: black dot; probable additional locality: ?) and the *Bothriurus bonariensis* group (*B. bonariensis*, squares; *B. chacoensis*, stars, and *B. jesuita*, triangles).

toni 2002a, 2002b, 2002c), and the patagonicus group (Mattoni & Acosta, unpub. data). The distribution of *B. pora* and the bonariensis group is congruent with the hypothesised relationships of the Cerrado with the Chaco, in a putative 'faunistic corridor' for scorpions ('corridor B' of Lourenço 1994). Moreover, the araguayae group, a probable sister group of the clade comprising *B. pora* and the bonariensis group (Mattoni 2003), shows a complementary pattern. The araguayae group is mainly distributed towards the center and north of the Cerrado, with one species inhabiting humid forests in the northern sector of the Argentine province of Misiones and the southwest part of Paraná State, Brazil (Lourenço & Maury 1979; Mattoni 2003).

Additional material examined (bonariensis group).—*Bothriurus bonariensis:* BRAZIL: *Estado do Rio Grande do Sul*: 1 ♀, Novo Hamburgo [24°41′09″S, 51°08′03″W], 22 November 1965, C. Valle (MZUSP 8682; 22); 1 ♂, Porto Alegre [30°02′09″S, 51°12′03″W], 14 March 1957, C. Schneider (MCN 0098); 1 juvenile, same locality, 1 April 1957, E.H. Buckup (MCN 0105); 1 ♂, Pavaela 44, Viamão [30°05′09″S, 51°02′04″W], 25 November 1956, M. Palova (MCN 0061); 1 juvenile, Ipanema, Porto Alegre [30°08′10″S, 51°13′49″W], 24 September 1956, M. Palova (MCN 0043); 1 juvenile, Ponta Grossa, Porto Alegre [30°02′S, 51°12′W], 21–26 June 1945, M.P. Godoi (MZUSP 13.736); 1 juvenile, same locality and collector, 1 June 1946 (MZUSP); 4 ♀, same locality and collector, cultivated land, rocks, 23 February 1945 (MZUSP 16.115); 6 ♂, Guaiba [30°06′50″S, 51°19′04″W], 27 February 1975, H.A. Gastal (MCN 0007); 2 ♂,

same locality and collector, 5 February 1975 (MCN 0028); 1 juvenile, Belem Novo [30°12′10″S, 51°10′04″W], 4 June 1946, M.P. Godoi (MZUSP 13.733); 1 ♂, São Leopoldo [29°46′05″S, 51°09′08″W], 15 November 1965, C. Valle (MZUSP); 3 ♂, Quarai [30°23′09″S, 56°27′03″W], February 1963, J.W. Thome (MCN 0019); 1 juvenile, Barra do Quarai [30°23′S, 56°27′W], 20 February 1974 (MZUSP); 1 juvenile, km 211, Pelotas [31°46′S, 52°20′W], 28 July 1965, Exped. CDZ (MZUSP). ARGENTINA: *Provincia de Córdoba*: 5 ♂, 1 juvenile, Toledo, 1 km road to Córdoba [31°34′S, 64°01′W], 24 January 1987, L. Acosta (CDA 000.101). URUGUAY: *Departamento Tacuarembó*: 1 juvenile, Tacuarembó [31°44′S, 55°59′W], 7 March 1944, E. Mullin-Díaz (MZUSP 8710).

Bothriurus chacoensis: ARGENTINA: *Provincia de Córdoba*: 6 ♂, 2 ♀, 3 juveniles, Eufrasio Loza, 3 km to Gutenberg [29°56′S, 63°35′W], 20 February 1987, L. Acosta, A. Peretti (CDA 000.103).

Bothriurus jesuita: ARGENTINA: *Provincia de Misiones*: 1 ♂, Campo San Juan, 37 km N Posadas by route N° 12 [27°20′S, 55°38′W], 21 January 1991, G. Flores (CDA 000.102).

ACKNOWLEDGMENTS

We are grateful to curators of the following institutions for the loan of specimens and for allowing access to their collections: Erika Buckup (MCN), Denise Candido (IBSP) and Ricardo Pinto-da-Rocha (MZUSP). CIM is especially indebted to Candido and Pinto-da-Rocha for their help, collaboration and company during his visit to São Paulo. We thank Lorenzo Prendini (American Museum of Natural History), Alfredo Peretti and Moira Battán-Horenstein (Cátedra de Diversidad Animal I, Universidad Nacional de Córdoba) for sharing unpublished information. This contribution is part of the Doctoral Thesis of CIM, carried out at Universidad Nacional de Córdoba (Argentina), under advice of LEA. Research partially supported by a grant of the University's Secretaría de Ciencia y Tecnología (Secyt) to LEA, and a Postgraduate grant from CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina) to CIM. LEA is researcher of CONICET.

LITERATURE CITED

Acosta, L.E. & E.A. Maury. 1998. Scorpiones. Pp. 545–559. *In* Biodiversidad de artrópodos argentinos. (J. J. Morrone & S. Coscarón, eds.). Ediciones Sur, La Plata, Argentina.

Acosta, L.E. & J.A. Ochoa. 2002. Lista de los escorpiones bolivianos (Chelicerata: Scorpiones), con notas sobre su distribución. Revista de la Sociedad Entomológica Argentina 61(3–4):15–23.

Acosta, L.E. & A.V. Peretti. 1998. Complemento a la descripción de *Bothriurus bonariensis* (Scorpiones, Bothriuridae) con anotaciones sobre patrones evolutivos del género en Argentina. Revue Arachnologique 12(10):95–108

Brazuna, J.C.M. & W.W. Koller. 1998. Escorpiões e escorpionismo na Área Urbana de Campo Grande, MS, Brasil. In: Seminário Nacional de Zoonoses e Animais Peçonhentos, 3, Guarapari, p: 1.

Cabrera, A.L. & A.W. Willink. 1980. Biogeografía de América Latina. Serie de Biología, OEA, monogr. 13, 122 pp.

Francke, O.F. 1977. Two emendations to Stahnke's (1974) Vaejovidae revision (Scorpionida, Vaejovidae). Journal of Arachnology 4:125–135.

Lourenço, W.R. & E.A. Maury. 1979. Quelques considérations sur la systématique du scorpion brésilien *Bothriurus araguayae* Vellard, 1934 (Bothriuridae). Bulletin du Muséum National d'Historie Naturelle, Paris (Zoologie, Biologie et Écologie Animales), 2:421–431.

Lourenço, W.R. 1994. Biogeographic patterns of tropical South American Scorpions. Studies on Neotropical Fauna and Environment 29(4):219–231.

Lowe, G. & V. Fet. 2000. Family Bothriuridae Simon, 1880. Pp. 17–53. *In* Catalog of the scorpions of the world (1758–1998). (Fet, V., Sissom, W. D., G. Lowe & M. E. Braunwalder eds.). The New York Entomological Society, New York.

Mattoni, C.I. & L.E. Acosta. 1997. Scorpions of the insular sierras in the Llanos District (Province of La Rioja, Argentina) and their zoogeographical links. Biogeographica 73(2):67–80.

Mattoni, C.I. 2002a. *Bothriurus picunche* sp. nov., a new scorpion from Chile (Scorpiones, Bothriuridae). Studies on Neotropical Fauna and Environment 37(2):169–174.

Mattoni, C.I. 2002b. La verdadera identidad de *Bothriurus vittatus* (Guérin Méneville, [1838]) (Scorpiones, Bothriuridae). Revue Arachnologique 14(5):59–72.

Mattoni, C.I. 2002c. *Bothriurus pichicuy* sp. nov., nuevo escorpión chileno del grupo *vittatus* (Scorpiones: Bothriuridae). Iheringia, Série Zoologia 92(4):81–87.

Mattoni, C.I. 2003. Patrones evolutivos en el género *Bothriurus* (Scorpiones, Bothriuridae): análisis filogenético. i-vii + 249 pp., Doctoral Thesis,

Fac. Cien. Exactas, Físicas y Nat., Univ. Nac. Córdoba, Argentina.

Maury, E.A. 1973. Los escorpiones de los sistemas serranos de la provincia de Buenos Aires. Physis, secc. C, 32(85):351–371.

Maury, E.A. 1979. Apuntes para una zoogeografía de la escorpiofauna argentina. Acta Zoológica Lilloana 35:703–719.

Maury, E.A. 1980. Usefulness of the hemispermatophore in the systematics of the scorpion family Bothriuridae. Pp. 335–339. *In* Verhandlungen. 8. Internationaler Arachnologen-Kongress. Abgehalten an der Universität fur Bodenkultur Wien, 7–12 Juli, 1980, H. Egermann, Vienna.

Maury, E.A. 1982. Dos *Bothriurus* del nordeste brasileño (Scorpiones, Bothriuridae). Revista de la Sociedad Entomológica Argentina 41(14): 253–265.

Maury, E.A. & L.E. Acosta. 1993. Un nuevo *Bothriurus* del grupo *bonariensis* (Scorpiones, Bothriuridae). Boletín de la Sociedad de Biología de Concepción 64:113–119.

Ojanguren Affilastro, A.A. 2002. Descripción de *Bothriurus pampa* sp. n., con nuevas localidades para el grupo *prospicuus* (Scorpiones, Bothriuridae). Revista Ibérica de Aracnología 6:95–102.

Ojanguren Affilastro, A.A. 2003. *Bothriurus jesuita*, a new scorpion species from norteastern Argentina (Scorpiones, Bothriuridae). Journal of Arachnology 31:55–61.

Peretti, A.V. 1992. El espermatóforo de *Bothriurus bonariensis* (C.L. Koch) (Scorpiones, Bothriuridae): morfología y funcionamiento. Boletín de la Sociedad de Biología de Concepción 63:157–167.

Peretti, A.V. & M. Battán-Horenstein. 2003. Comparative analysis of the male reproductive system in Bothriuridae scorpions: structures associated with the paraxial organ and the presence of sperm packages (Chelicerata, Scorpiones). Zoologischer Anzeiger 242:21–31.

Prendini, L. 2000. Phylogeny and classification of the superfamily Scorpionoidea Latreille 1802 (Chelicerata, Scorpiones): an exemplar approach. Cladistics 16:1–78.

Prendini, L. 2003. A new genus and species of bothriurid scorpion from the Brandberg Massif, Namibia, with a reanalysis of bothriurid phylogeny and a discussion on the phylogenetic position of *Lisposoma* Lawrence. Systematic Entomology 28:149–172.

San Martín, P.R. 1963. Una nueva especie de *Bothriurus* (Scorpiones, Bothriuridae) del Uruguay. Bulletin du Muséum National d'Historie Naturelle, Paris (2) 35:400–418.

San Martín, P.R. 1965. Escorpiofauna Uruguaya II. *Bothriurus rochensis*, nueva especie de Bothriuridae del Uruguay. Comunicaciones Zoológicas del Museo de Historia Natural de Montevideo 8(106):1–22.

Sissom, W.D. 1990. Systematics, biogeography and paleontology. Pp. 64–160. *In* The Biology of Scorpions. (G.A. Polis ed.). Stanford University Press, Stanford, California.

Stahnke, H.L. 1970. Scorpion nomenclature and mensuration. Entomological News 81:297–316.

Vachon, M. 1974. Étude des caractères utilisés pour classer les familles et les genres de scorpions (Arachnides). 1. La trichobothriotaxie en Arachnologie. Sigles trichobothriaux et types de tricobothriotaxie chez les Scorpions. Bulletin du Muséum National d'Historie Naturelle, Paris (3) 140:857–958.

Manuscript received 2 June 2004, revised 20 September 2004.

2005. The Journal of Arachnology 33:745–752

DIEL ACTIVITY PATTERNS AND MICROSPATIAL DISTRIBUTION OF THE HARVESTMAN *PHALANGIUM OPILIO* (OPILIONES, PHALANGIIDAE) IN SOYBEANS

Cora M. Allard and **Kenneth V. Yeargan**: Department of Entomology, University of Kentucky, S-225 Ag Science North, Lexington, KY 40506 USA. E-mail: cmallard_22@hotmail.com

ABSTRACT. *Phalangium opilio* L. is a polyphagous predator frequently found in agricultural habitats. Although the potential importance of *P. opilio*'s feeding on pests has been recognized, little is known about its activity patterns or its within-plant distribution in crops. We determined diel activity patterns and microspatial distribution in small, fenced arenas in soybean fields. The fenced arenas allowed us to track known numbers of particular size categories of *P. opilio* for each 24 h trial. *Phalangium opilio* were separated into the following categories based on body size and sex: medium-sized nymphs, large-sized nymphs, adult females and adult males. Medium-sized nymphs occupy the bottom and middle portions of plants regardless of time of day; they remain still during the day, but they exhibit leg palpating behavior from 21:00–01:00 h. Large-sized nymphs rest in the bottom and middle portions of plants during the day, but they walk and palpate on the ground from 21:00–01:00 h. Adult females rest in the bottom, middle and top portions of plants during the day, and they walk and palpate on the ground from 21:00–01:00 h. Adult males remain stationary in the bottom, middle and top portions of plants during the day, but they walk on the ground from 21:00–04:00 h.

Keywords: Predator, behavior, microhabitat separation

The microspatial distribution and diel activity patterns of predators in crops affect the prey they encounter, which potentially affects their value in biological control. When different instars of the same species separate their location and activities spatially and temporally, the separation may reduce cannibalism and/or intraspecific competition for resources. All these factors have the potential to affect the population dynamics of arthropod species in agricultural systems. Predatory members of the group Opiliones are sometimes overlooked in crops. One such predator is *Phalangium opilio* L. 1758. We studied *P. opilio*'s microspatial distribution and diel activity because of its potential importance in biological control of soybean pests (Anderson 1996; Pfannenstiel & Yeargan 2002).

Microhabitat separation of different life stages is seen in some Opiliones. For example, *Mitopus morio* (Fabricius 1799) exhibits vertical stratification, with late instars found at high vegetation strata (Adams 1984). Vertical distribution of *P. opilio* is believed to vary among habitats. When sparse shrub cover is present, 88% of *P. opilio* are found in shrubs and brushy vegetation, but with dense cover, the highest percentage of *P. opilio* is found on the ground layer (Edgar 1980). Cloudsley-Thompson (1968) also observed *P. opilio* to primarily inhabit low vegetation or grass and other herbaceous plants, but he stated that the early instars only occur on the ground. Several hypotheses have been presented to explain microhabitat separation in Opiliones. Opilionids may be found on vegetation to eliminate competition with strict ground predators (Halaj & Cady 2000). It also has been hypothesized that the vertical expansion of the distribution of late instars is due to the need for larger prey, more moving space, mating, and/or different temperature and humidity requirements (Sankey 1949; Todd 1949). Not all individuals abandon the ground; Williams (1962) found individuals of the same species and instar both in pitfall traps and on vegetation. Based on those results, Williams hypothesized opilionids may expand their microhabitat distribution

without completely abandoning the ground. However, it is possible that Williams' (1962) results reflected diel movement, not microhabitat separation.

Opiliones generally are nocturnal (Sankey 1949; Todd 1949; Phillipson 1960; Williams 1962; Edgar & Yuan 1969). The increase in activity at night may be attributed to decreased light intensity, increased relative humidity and decreased temperatures (Todd 1949). Pfannenstiel & Yeargan (2002), who observed predation events on *Helicoverpa zea* (Boddie 1850) eggs in soybean fields at 3 h intervals during 24 h cycles, found that all observed events of predation by Phalangiidae occurred at night. Although *P. opilio* occasionally is active under diurnal conditions, individuals exhibit 90% of their total activity between 1800–0600 h (Edgar & Yuan 1969; Edgar 1980).

Phalangium opilio is known to feed, primarily nocturnally, upon a variety of arthropod pests. In Kentucky, this predator appears to overwinter in the egg stage and undergo three generations per year (Newton & Yeargan 2002), with the second generation being the most relevant to predation in soybean (due to seasonal timing of this annual crop), where it feeds on *H. zea* eggs (Pfannenstiel & Yeargan 2002). Other aspects of its ecology relevant to its role in soybean fields are poorly known, including its diet breadth, its spatial distribution in large fields, its within-plant/epigeal distribution and its diel activity patterns. We investigated the diel activity patterns and microspatial distribution of *P. opilio* for nymphal instars three through seven and both adult sexes.

METHODS

This study was done during the summers of 2001 and 2002 at the University of Kentucky's North Farm near Lexington, KY. In each year, three small plots (1 m of soybean row per plot) were established within a 0.6 ha field of soybeans. The soybean variety used in both years was Asgrow 4702 and planting occurred on 1 May 2001 and 20 May 2002. Each 1 m plot was surrounded by a fence of galvanized sheet metal (20 cm tall, 0.5 m from plants on either side of fence); preliminary studies showed *P. opilio* could not scale this fence. In both years, the entire soybean field was treated at planting with recommended rates of conventional pre-emergence herbicides (alachlor, metribuzin and chlorimuron ethyl) and was subsequently treated once (2002) or twice (2001) with the post-emergence herbicide glyphosate for additional weed control. Post-emergence herbicide treatments occurred several weeks before trials began. No insecticides were applied during either year. Trials were conducted weekly from 23 July–9 September 2001 and from 7–24 August 2002.

Phalangium opilio were collected in the field no more than 5 d prior to the trial dates. Individuals were taken to the laboratory, measured and/or sexed in order to be placed in a category (described below), and provided with food (i.e., *H. zea* eggs and cornmeal/bacon diet) and water; food was removed 24 h prior to the initiation of observations and individuals were marked with a small dot of paint 12 h prior to the initiation of field observations. In the laboratory, individuals were kept in 8.5 × 8.5 cm (diam × ht) containers in incubators at 24 ± 1 °C (15:9 L:D) with high humidity via open water containers on the floor of the incubators. Prior to the initiation of trials, field arenas were checked for naturally occurring opilionids that were removed when found. No opilionid species other than *P. opilio* were encountered in this study. No other potential prey were removed from or added to an arena. Three arenas were monitored on each date. In each arena, three field collected *P. opilio* of the same category marked with pink fluorescent, water-based paint (Apple Barrel Colors, Plaid Enterprises, Inc.) were introduced simultaneously on the ground in the center of an arena 1 h before observations began. There is no accurate morphological indicator for sex or instar in *P. opilio* nymphs; therefore, size categories (hereafter referred to as *P. opilio* categories) based on cephalothorax width were used (after Newton & Yeargan 2002). Small nymphs were less than 1.0 mm, medium nymphs ranged from 1.0–1.5 mm, and large nymphs were greater than 1.5 mm in cephalothorax width. Adults were discriminated from nymphs based on the presence or absence of a genital opening beneath the operculum (Sankey & Savory 1974) and adult males and females were identified based on the presence or absence of the sexually dimorphic horns on the distal segment of male chelicerae (Sankey & Savory 1974).

During the trials, 5 min observations were made at each arena at 20 min intervals for 1 h at approximately: 1200, 1500, 1800, 2100, 0000, 0300 and 0600 h (EDT). A red light filter, which minimized disturbance to the animals, was used to make nocturnal observations and an ultraviolet light was used to locate individuals only if they could not be found with the red light. The ultraviolet light was used for ≈10% of the observations. During each observation, the location of individuals (i.e., on ground or plant; if on plant, bottom, middle, or top third of the plant, and exterior or interior portion of the plant) and the behavior of individuals (i.e., walking, grooming, feeding, stationary, palpating, drinking) were recorded. Exterior and interior portions of the plants were differentiated based on whether or not the view of the observer was obstructed by other plant parts (i.e., if an opilionid was on a plant part that had no other plant part between it and the observer, it was recorded as being on the exterior). For the purposes of this study, palpating behavior is defined as the movement of the sensory legs (i.e., the long second pair) in a slow tapping motion on the surrounding substrate. All behaviors recorded were mutually exclusive, and only the first observation of an individual was recorded within each 5 min observation period.

Each trial consisted of three individuals observed in a field arena for 24 h. In 2001, the following number of trials were conducted: small-sized nymphs (n = 1), medium-sized nymphs (n = 6), large-sized nymphs (n = 4), adult females (n = 5), and adult males (n = 5). In 2002, the following number of trials were conducted: medium-sized nymphs (n = 1), large-sized nymphs (n = 3), adult females (n = 2), and adult males (n = 2). Small nymphs were excluded from the study after the first trial due to the difficulty in seeing the nymphs, due in part to their tendency to hide in tiny crevices. The combined years yielded seven trial dates for all *P. opilio* categories excluding small. After each trial date, all individuals were removed from the arenas and nymphs were reared in the laboratory until maturity for positive identification to species. Individuals were not always found at the time of observations, but all individuals were recovered at the end of each trial. Voucher specimens were placed in the arthropod collection of the Department of Entomology at the University of Kentucky.

Statistical analysis.—In order to analyze the microspatial distribution and behaviors for the different nymphal and adult *P. opilio* categories, proportions were calculated for each set of three individuals during each 1 h observation period. There was a maximum of nine observations per arena per hour (i.e., three individuals times three visits = the denominator for calculating proportions). These proportions reflected the frequency of observations of *P. opilio* at a particular place (ground, bottom of plant, middle of plant, top of plant) or engaged in a particular behavior (stationary, walking, feeding, palpating, drinking).

Category X time interactions were examined to determine if different *P. opilio* categories (medium-sized nymphs, large-sized nymphs, adult males and adult females) were at different locations at different times of the day and if they exhibited different behaviors. Because the ANOVA assumptions of homogeneity of variances and normality of the variables were not met, even after several transformations, we used profile analysis, which can be performed with both parametric and non-parametric statistics to test for the category X time interactions (Ende 1993). To compute a profile analysis the response variable (i.e., percentage of time per hour) was subtracted between repeated measures and tested for differences among *P. opilio* categories on the resulting variable. The new variables did not meet the ANOVA assumptions; therefore, the non-parametric Kruskal-Wallis ANOVA (Siegel & Castellan 1988) was used to test for differences among *P. opilio* categories with the new (subtracted) variables. There were seven time periods. Six new variables were calculated for the profile analysis performed on each location and behavior. Each variable was derived by subtracting the response variable (i.e., percentage of time per hour) of every time period from the response at one arbitrarily selected time period (i.e., 00:00 h). Thus, the first variable for profile analysis was 00:00 minus 03:00 h, the second was 00:00 minus 06:00 h, and so on. This allowed interactions to be detected and showed which time periods had a larger change in location or behavior. Therefore, we tested for significance of six variables, four locations and five

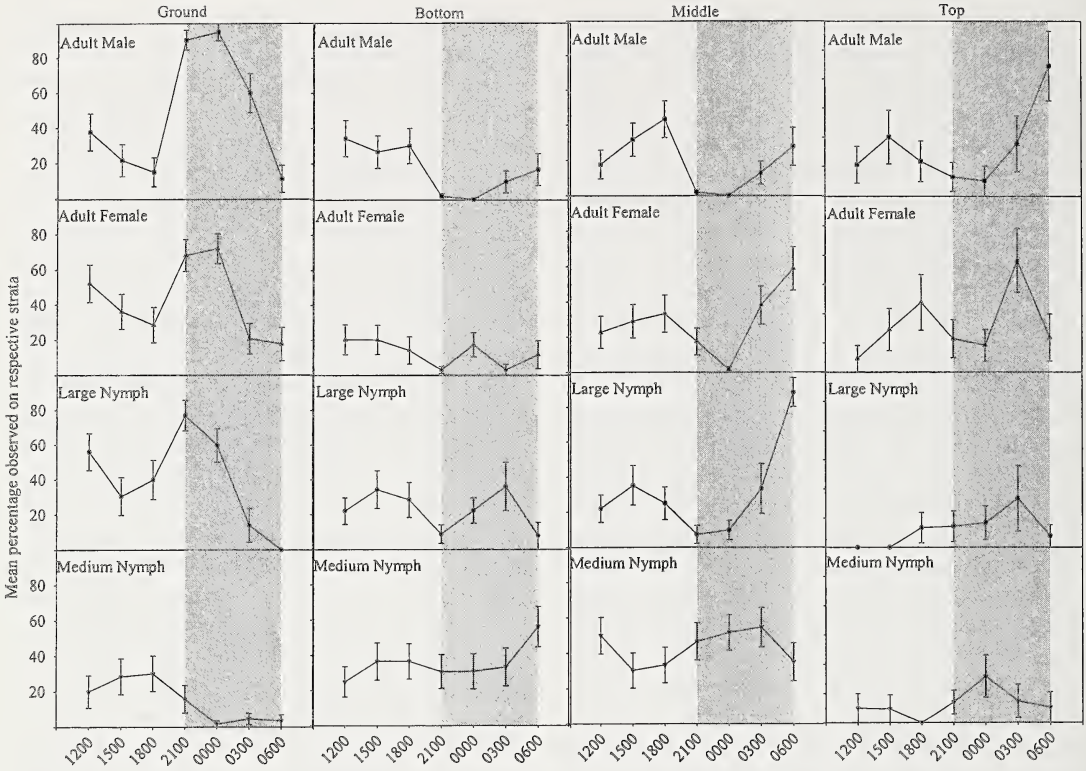


Figure 1.—Percentage of observations (mean ± SE) for all *Phalangium opilio* categories on the ground, in the bottom, in the middle, and in the top portions of soybean plants during diurnal (not shaded) and nocturnal (shaded) hours.

behaviors, for a total of $6 \times (4+5) = 54$ tests. Because significance of the overall category X time interaction could not be tested as it is done in repeated measures ANOVA, the criterion to decide whether there was an overall significant interaction for each category and location or behavior was whether a combined probability test (Fisher's meta-analysis; Sokal & Rohlf 1995) across the six tests was significant. The resulting value is compared with the chi-square distribution with twice as many degrees of freedom as number of tests performed (in this case $2 \times 6 = 12$ d.f.).

To test if, at different heights, the different *P. opilio* categories were more likely located on the exterior or in the interior part of the plant, a logistic regression analysis was used. The response variable was interior or exterior on the plant, which were coded as 0 and 1 respectively. For this analysis the data for all time periods were pooled and the frequency at which individuals were on the interior or exterior of the plant at every height was included in the model by using the FREQ statement in the SAS LOGISTIC procedure (Allison 1999). For graphical purposes, the percentage of time per hour in which individuals were exterior at every height was averaged across individuals. A significant category X height interaction in the logistic regression indicates that there is spatial segregation in relation to exterior and interior portions of the plant and that it is different at different heights.

RESULTS

There was a significant category X time interaction for all vertical strata (i.e., ground, bottom, middle and top) indicating that different *P. opilio* categories were at different strata at different times (Fig. 1; Table 1). All *P. opilio* categories, excluding medium-sized nymphs (which remained on the plants), moved to the ground at nightfall, 21:00 h, where they remained until 03:00 h. Males were on the ground significantly more than the females, and large nymphs and males remained on the ground in the 03:00 h when the

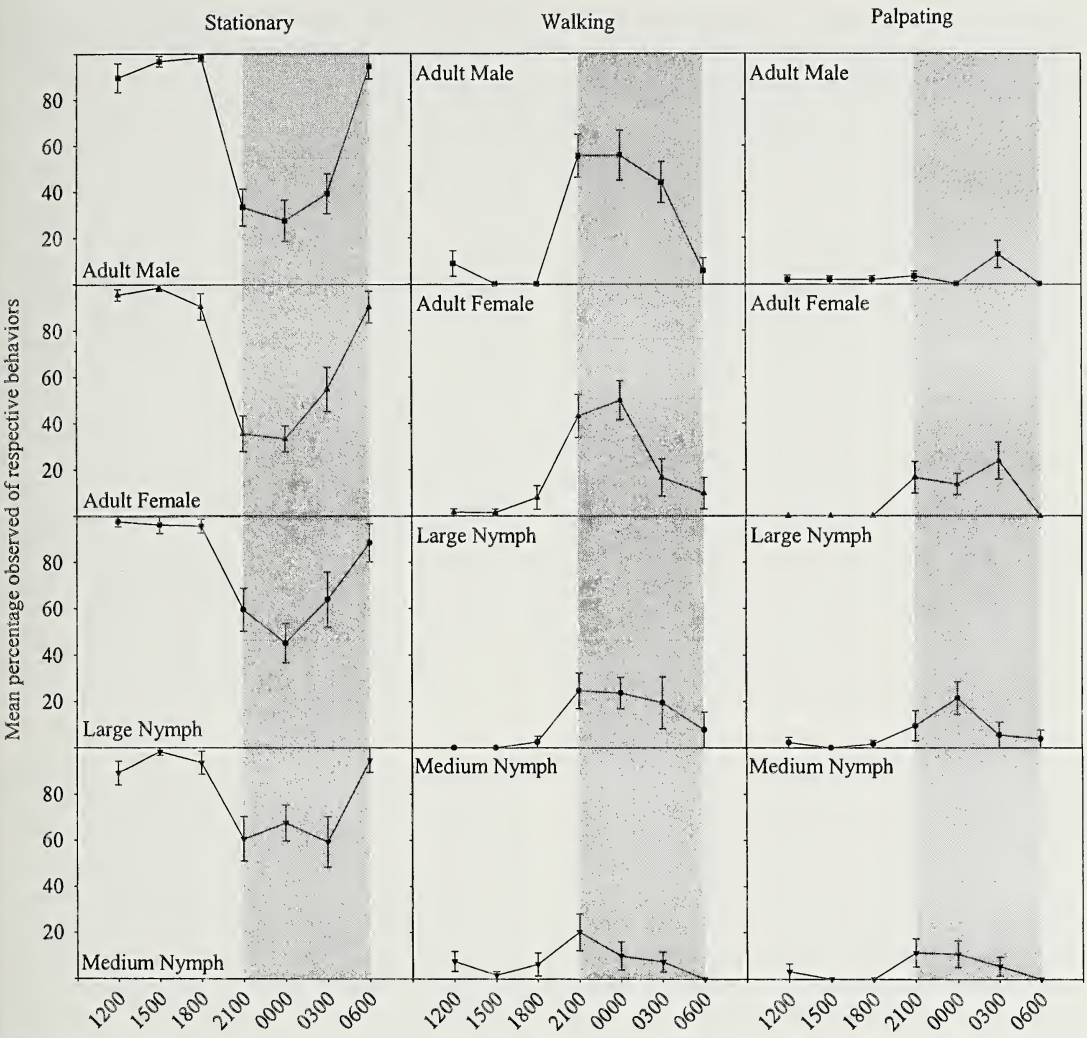


Figure 2.—Percentage of observations (mean ± SE) for all *Phalangium opilio* categories that were stationary, walking, and palpating in soybean plots during diurnal (not shaded) and nocturnal (shaded) hours.

females and large nymphs returned to the plants (Fig. 1). For the majority of the day all *P. opilio* categories were found on the plants. During this time, all *P. opilio* categories were recorded in the bottom and middle portions of the plants; however, small percentages of males and females were recorded in the top portion of the plants during the 15:00 and 18:00 h, respectively. Medium-sized nymphs remained on the bottom and middle portions of the plants at night. Early in the morning there was an increase in large nymph and female observations in the middle portions of the plants. A substantial percentage of the females was found on the top portion of the plants only during 03:00 h, followed by males at 06:00 h.

There also were significant category X time interactions for the following behaviors: stationary, walking, and leg palpating (Fig. 2; Table 1). Drinking, feeding and grooming were excluded because there were only a few recorded observations. Only a single case of predation was observed, namely a large immature individual feeding on an immature leafhopper (Hemiptera, Cicadellidae) on a soybean plant. The majority of all *P. opilio* categories were stationary during the day but stationary behavior was less common in the nocturnal hours. Virtually no walking behav-

Table 1.—Results from the Kruskal-Wallis ANOVA by ranks for the overall response of size and gender categories (average across time) of *Phalangium opilio* to heights on soybean plants and behaviors. Palpating = leg palpating.

	Ground		Bottom		Middle		Top	
Time periods	H	*p*	H	*p*	H	*p*	H	*p*
0000 minus 0300 h	5.738	0.125	5.564	0.135	5.738	0.125	8.287	0.041
0000 minus 0600 h	37.052	<0.001	9.396	0.025	12.908	0.005	13.782	0.003
0000 minus 1200 h	16.835	0.001	7.745	0.052	2.883	0.410	3.418	0.332
0000 minus 1500 h	27.552	<0.001	4.358	0.225	13.443	0.004	6.985	0.072
0000 minus 1800 h	33.475	<0.001	5.872	0.118	12.923	0.005	7.069	0.070
0000 minus 2100 h	1.308	0.727	4.811	0.186	4.047	0.256	2.491	0.477
Combined test		<0.001		0.006		<0.001		0.001

	Stationary		Walking		Feeding		Palpating		Drinking	
Time periods	H	*p*	H	*p*	H	*p*	H	*p*	H	*p*
0000 minus 0300 h	5.509	0.138	6.691	0.083	8.326	0.040	11.239	0.011	1.166	0.761
0000 minus 0600 h	10.667	0.014	15.569	0.001	7.822	0.050	8.889	0.031	1.911	0.591
0000 minus 1200 h	10.008	0.019	18.396	<0.001	8.854	0.031	10.568	0.014	1.911	0.591
0000 minus 1500 h	12.740	0.005	19.336	<0.001	7.965	0.047	12.290	0.007	1.911	0.591
0000 minus 1800 h	8.951	0.030	18.334	<0.001	8.854	0.031	10.218	0.017	1.911	0.591
0000 minus 2100 h	0.932	0.818	1.096	0.778	4.179	0.243	6.406	0.094	0.538	0.911
Combined test		0.000		<0.001		0.000		<0.001		0.960

ior was exhibited during the day, but with nightfall there was a large increase in walking behavior for males and females and a small increase for nymphs. Males and females exhibited walking behavior from nightfall through the midnight hour, and males continued walking through the early morning, 03:00 h, while female walking decreased. None of the *P. opilio* categories exhibited leg palpating during the day. Large nymphs showed a peak in leg palpating during the midnight hour, and medium nymphs exhibited a small amount of leg palpating from nightfall through the midnight hour. Females exhibited leg palpating at night, and males showed a small peak in leg palpating at 03:00 h but not at any other time.

The percentage of *P. opilio* categories found on the exterior, as opposed to the interior, of plants varied with height on the plant and *P. opilio* category. Some *P. opilio* categories tended to be on the exterior or on the interior of the plant at a relatively different rate from each other at different heights. The full logistic regression model was highly significant ($\chi^2_{11} = 157.3$, $P < 0.001$). Both the category ($\chi^2_3 = 21.2$, $P < 0.001$) and the height ($\chi^2_2 = 31.8$, $P < 0.001$) effects were significant, as well as the interaction term between them ($\chi^2_6 = 27.2$, $P < 0.001$). In the bottom portion of the plants, all *P. opilio* categories tended to stay in the interior of the plant. In the middle portion of the plant, some individuals were found on the exterior, with the notable exception of large nymphs, which were almost exclusively found in the interior. Except for adult males, individuals of all other categories were found on the exterior more frequently in the top portion of the plant than in either of the other two plant strata (Fig. 3).

DISCUSSION

Nymphal *P. opilio* were somewhat more restricted than adult *P. opilio* in their microspatial distribution. Although distribution of adult males and females changed over the diel cycle, they were found on the ground and in all plant strata. Large nymphs, however, were seldom found in the top portion of plants. Medium nymphs appeared to be even more restricted, primarily occurring on the middle and lower portions of plants. The restricted distribution of nymphs may reduce encounters with adult *P. opilio*.

Phalangium opilio became active with the onset of nightfall (21:00 h). At this time all *P. opilio*, excluding the medium-sized nymphs, moved to the ground. Medium-sized nymphs might suffer higher predation risks

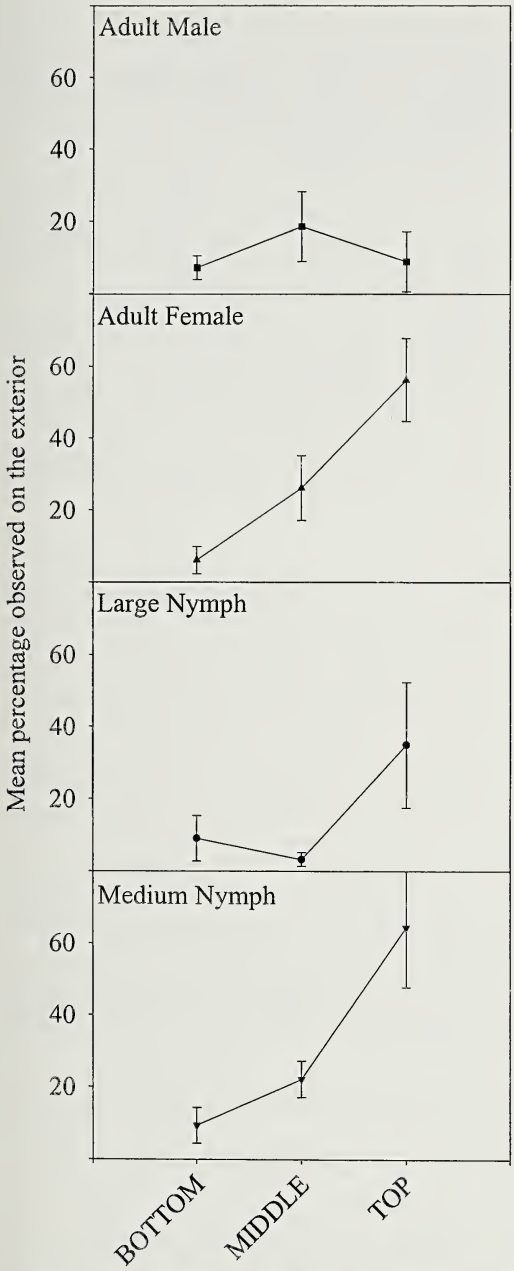


Figure 3.—Percentage of observations (mean ± SE) for all *Phalangium opilio* categories that were on the exterior of soybean plants as opposed to the interior of the plants at different heights.

from other nocturnal ground predators, as well as larger *P. opilio*, which may account for their tendency to remain in the vegetation. While on the ground, *P. opilio* remains active. Males spent most of their time walking and little time palpating. Females also spent considerable time walking on the ground but also spent time palpating. Nymphs spent less time walking than adults, with medium nymphs walking the least of all *P. opilio* categories. Adult females and nymphs engaged in palpating behavior more frequently than did adult males.

If palpating is a foraging strategy in this species, it is not surprising that females and nymphs were observed palpating more than males. Adult females need nutrients to invest in reproduction, and nymphs need nutrients for development, while adult males presumably need less nutrients. It might be expected that adult males would spend more time walking in search of female mates. Females lay eggs in the soil, so the marked tendency for males to spend more time walking on the ground (Fig. 1) may increase their likelihood of encountering females there.

Since *P. opilio* is known to feed on *H. zea* eggs in soybean fields (Anderson 1996; Newton & Yeargan 2001; Pfannenstiel & Yeargan 2002), it is worthwhile to consider the microspatial distribution of *P. opilio* compared to that of *H. zea* eggs in soybean. Terry et al. (1987) observed that *H. zea* oviposited throughout the vertical strata of soybean plants, with approximately 70% of the eggs being laid on main-stem leaves. Hillhouse & Pitre (1976) reported that the upper and middle thirds of the soybean plants were preferred for oviposition compared to the lower third. The microspatial distribution of *P. opilio* does overlap with the distribution of *H. zea* eggs.

Knowledge of the distribution and behavior of *P. opilio* is important in assessing its potential impact on arthropod pests in soybean systems. Its stage-specific activity patterns and distributions may affect reproductive opportunities, intraspecific competition, cannibalism, and potential encounters with prey species.

ACKNOWLEDGMENTS

The authors thank Jordi Moya-Loraño for his statistical advice. The authors also thank Kenneth Haynes and Janet Lensing for reviewing an earlier version of the manuscript. This investigation (paper no. 04-08-049) was conducted in connection with a project of the Kentucky Agricultural Experiment Station.

LITERATURE CITED

Adams, J. 1984. The habitat and feeding ecology of woodland harvestmen (Opiliones) in England. Oikos 42:361–370.

Allison, P.D. 1999. Logistic regression using the SAS system: theory and application. SAS Institute Inc., Cary, NC.

Anderson, A. 1996. Influence of soybean canopy closure on generalist predator abundance and predation on corn earworm eggs. Master's thesis, University of Kentucky, Lexington, KY.

Cloudsley-Thompson, J.L. 1968. Spiders, scorpions, centipedes, and mites. Pergamon Press, New York.

Edgar, A.L. 1980. Physiological and ecological aspects of the cosmopolitan opilionid, *Phalangium opilio*. Pp 170–180. *In* Soil Biology as Related to Land Use Practices. Proceedings of the VIIth International Colloquia of Soil Biology, International Society of Soil Science, Washington, District of Columbia.

Edgar, A.L. & H.A. Yuan. 1969. Daily locomotory activity in *Phalangium opilio* and seven species of *Leiobunum* (Arthropoda: Phalangida). Bios 39:167–176.

Ende, C.N. 1993. Repeated-measures analysis: growth and other time-dependent measures. Pp. 113–137. *In* S. M. Schneiner and J. Gurevitch (eds.), Design and Analysis of Ecological Experiments. Chapman and Hall, New York.

Halaj, J. & A.B. Cady. 2000. Diet composition and significance of earthworms as food of harvestmen (Arachnida: Opiliones). American Midland Naturalist 143:487–491.

Hillhouse, T.L. & H.N. Pitre. 1976. Oviposition by *Heliothis* on soybeans and cotton. The Journal of Economic Entomology 69:144–146.

Newton, B.L. & K.V. Yeargan. 2001. Predation of *Helicoverpa zea* (Lepidoptera: Noctuidae) eggs and first instars by *Phalangium opilio* (Opiliones: Phalangiidae). The Journal of the Kansas Entomological Society 74:199–204.

Newton, B.L. & K.V. Yeargan. 2002. Population characteristics of *Phalangium opilio* (Opiliones: Phalangiidae) in Kentucky agroecosystems. Environmental Entomology 31:92–98.

Pfannenstiel, R.S. & K.V. Yeargan. 2002. Identification and diel activity patterns of predators attacking *Helicoverpa zea* (Lepidoptera: Noctuidae) eggs in soybean and sweet corn. Environmental Entomology 31:232–241.

Phillipson, J. 1960. A contribution to the feeding biology of *Mitopus morio* (F.) (Phalangida). Journal of Animal Ecology 29:35–43.

Sankey, J.H.P. 1949. British harvest-spiders. Essex Naturalist 28:181–191.

Sankey, J.H.P. & T.H. Savory. 1974. British harvestmen. Synopsis of the British Fauna, No. 4. Academic Press, London.

SAS Institute. 2000. Software release 8.0. Cary, North Carolina.

Siegel, S. & N.J. Castellan. 1988. Non-parametric statistics for the behavioral sciences. McGraw-Hill International Editions, New York.

Sokal, R.R. & F.J. Rohlf. 1995. Biometry: the Principles and Practice of Statistics in Biological Research. W.H. Freeman, New York.

Terry, I., J.R. Bradley,Jr. & J.W. Van Duyn. 1987. With-in plant distribution of *Heliothis zea* (Boddie) (Lepidoptera: Noctuidae) eggs on soybeans. Environmental Entomology 16:625–629.

Todd, V. 1949. The habits and ecology of the British harvestmen (Arachnida, Opiliones), with special reference to those of Oxford District. Journal of Animal Ecology 18:209–229.

Williams, G. 1962. Seasonal and diurnal activity of harvestmen (Phalangida) and spiders (Araneae) in contrasted habitats. Journal of Animal Ecology 31:23–42.

Manuscript received 24 March 2004, revised 9 July 2004.

2005. The Journal of Arachnology 33:753–757

IDENTITY AND PLACEMENT OF SPECIES OF THE ORB WEAVER GENUS *ALCIMOSPHENUS* (ARANEAE, TETRAGNATHIDAE)

Herbert W. Levi: Museum of Comparative Zoology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts 02138-2902, U.S.A. E-mail: levi@fas.harvard.edu

ABSTRACT. Species placed in the genus *Alcimosphenus* are examined. *Alcimosphenus licinus* Simon 1895 is redescribed and validated. *Alcimosphenus bifurcatus*, *A. rufoniger*, *A. boringuenae*, *Acusilas rufonigra* and *A. r. maculata* are placed in synonymy. *Alcimosphenus rubripleuris* Mello-Leitão is transferred to *Leucauge* and redescribed.

Keywords: Greater Antilles, species placement, Tetragnathidae

When consulted about the correct specific name for species within the genus *Alcimosphenus* Simon 1895, the common, orange-red orb weaving spider of the Greater Antilles, I found two specific names listed in Roewer (1942), and six in the World Spider Catalog (Platnick 2004). Simon's (1895) Latin description of the genus is short and indicates that specimens of *A. licinus* Simon 1895 from Jamaica and Santa Dominica may come with a forked posterior tip. In 1910, Petrunkevitch described *A. bifurcatus* from Jamaica but indicated that they were immature and smaller in size than *A. licinus* Simon. The name *A. bifurcatus* suggests forked, and it may be assumed that the name referred to specimens with a forked tail rather than a simple tail. That the species has a forked tail is confirmed in Petrunkevitch's (1930) key to Puerto Rican tetragnathids, which separates the two species, *A. licinus* with a pointed tail from *A. bifurcatus* with a forked tail. Again only immatures of *A. bifurcatus* were found, with forked tails, this time one from Mayagüez, Puerto Rico. In the same year Franganillo Balboa described a species from Cuba placed in *Acusilas* Simon 1895 (Araneidae). Later Franganillo (1936), placed it in *Alcimosphenus*, presumably not having seen Petrunkevitch's descriptions; it differed from *A. licinus*, having only a single tip. Although no male had been collected previously, Archer (1951) placed *Alcimosphenus* into the Araneidae close to *Arachnura* based on the description of a male in his collection (without locality). He later (Archer 1958) referred to the described male as coming from South America (no locality). Mello-Leitão (1947) described *A. rubripleurus* from the state of Paraná, Brazil. (It is often difficult to associate tetragnathids males with females even when collected close to the collecting site of the female, and examination of the Mello-Leitão specimen, which I examined, showed that it belongs in *Leucauge* White 1841). In 1958 Archer reported finding a mature female of *A. bifurcatus*, at last, from Hardwar Gap in Jamaica. He illustrated, poorly, its epigynum and that of *A. licinus*. Later in 1965, Archer found a female in Puerto Rico, with a barely visible tail division and slightly different epigynal proportions and gave it a new name, *A. borinquenae*.

Having now examined the original specimens of *A. licinus*, apparently the first time they have been examined since Simon, I found them to come from Jamaica, and all eight syntypes have forked tails (Figs. 1, 3). Two syntypes of *A. rufonigra* Franganillo 1930 from Cuba exist, each showing the single tip. Archer's male, belonging to the AMNH, was unavailable (presumably lost?), but judging from the description of the palpus, the primitive illustration, and its presumably red color and tail, it was a species of *Alpaida* O.P.-Cambridge 1889.

Simon, like many other 19th century authors, did not mark specimens as types and did not indicate the date collected on his labels. When borrowing from the Simon collection one can only hope that the original specimens, the types, have been sent. Scharff (pers. comm.) indicates that in examining the

catalog of the Paris collection, he found that specimens exist other than the ones examined.

On examining the contents of the 28 vials of *Alcimosphenus* of the MCZ collection, many with several specimens, I found that some are with a forked tail tip, some with a single tip. The forked tail specimens came mostly from Jamaica, but one immature was from Cuba; Petrunkevitch (1930) had one from Puerto Rico. There is considerable geographic variation of the proportions of the epigynum, the black patches, and the tail shape, but I find it difficult to separate specimens into different species using the epigynum. No males have ever been found, although I searched unsuccessfully for males in Puerto Rico and the collections of the American Museum.

Both *Leucauge* and *Alcimosphenus* differ from all other tetragnathids by having two parallel rows of trichobothria on the fourth femur, which appears to represent a synapomorphy. *Alcimosphenus* differs from *Leucauge* by having the anterior eye row straight; whereas *Leucauge* has the anterior eye row recurved (Simon 1895). According to Petrunkevitch (1930), *Alcimosphenus* differs by having the abdomen red and legs short; in *Leucauge* the abdomen is not red and the legs are longer. *Alcimosphenus* belongs in the family Tetragnathidae, judging by the shape of the endites (Fig. 4) and its superficial similarity to *Leucauge*, and had always been placed in Tetragnathidae before Archer (1951).

Griswold et al. (1998) and Hormiga et al. (1995) in their cladistic studies separate Araneidae from other araneoid families including Tetragnathidae by loss of the aciniform brush of the posterior median spinnerets, the peripheral position of the spigot of the cylindrical gland on the posterior lateral spinnerets and the use of the inner leg tap of the first leg used to determine the next point of attachment of the viscid web spiral. Tetragnathidae, in turn, is separated from other araneoid families by the conductor that wraps around the embolus, the presence of an embolus-tegulum membrane and the loss of the median apophysis of the male palpus. All characters are considered synapomorphies.

Abbreviations for museums where types are deposited: AMNH, American Museum of Natural History, New York; IESC, Instituto de Ecologia y Sistemática, La Habana, Cuba; MCZ, Museum of Comparative Zoology, Cambridge; MHNC, Museu de História Natural "Capão da Imbuia", Curitiba, Brazil; MNHN, Museum National d'Histoire Naturelle, Paris; YPM, Peabody Museum, Yale University, New Haven.

TAXONOMY

Family Tetragnathidae Menge 1866
Genus *Alcimosphenus* Simon 1895

Alcimosphenus Simon 1895: 931.

Type species.—*Alcimosphenus licinus* Simon 1895, by monotypy.

Description.—As the genus has now become monotypic, the species description can be used.

Alcimosphenus licinus Simon 1895
Figs. 1–7

Alcimosphenus licinus Simon 1895: 931; Simon 1897: 871; Petrunkevitch 1910:210; Petrunkevitch 1930:263, figs. 115, 116; Roewer 1942:999; Platnick 2004.

Alcimosphenus bifurcatus Petrunkevitch 1910:211, plate 21, fig. 8; Petrunkevitch 1930:264, figs. 117, 118; Roewer 1942:998; Platnick 2004. NEW SYNONYMY.

Acusilas rufonigra Franganillo Balboa, 1930:70. NEW SYNONYMY.

Acusilas rufonigra maculata Franganillo Balboa 1930:70. NEW SYNONYMY.

Alcimosphenus rufoniger: Franganillo Balboa 1936: 87, fig. 42; Platnick 2004.

Alcimosphenus boringuenae Archer, 1965:131, fig. 4; Platnick 2004. NEW SYNONYMY.

Type specimens.—*Alcimosphenus licinus*: 4 female, 4 immature syntypes, Jamaica (MNHN, no. 15818), examined. [Syntypes originally from Jamaica and Santa Dominica.]

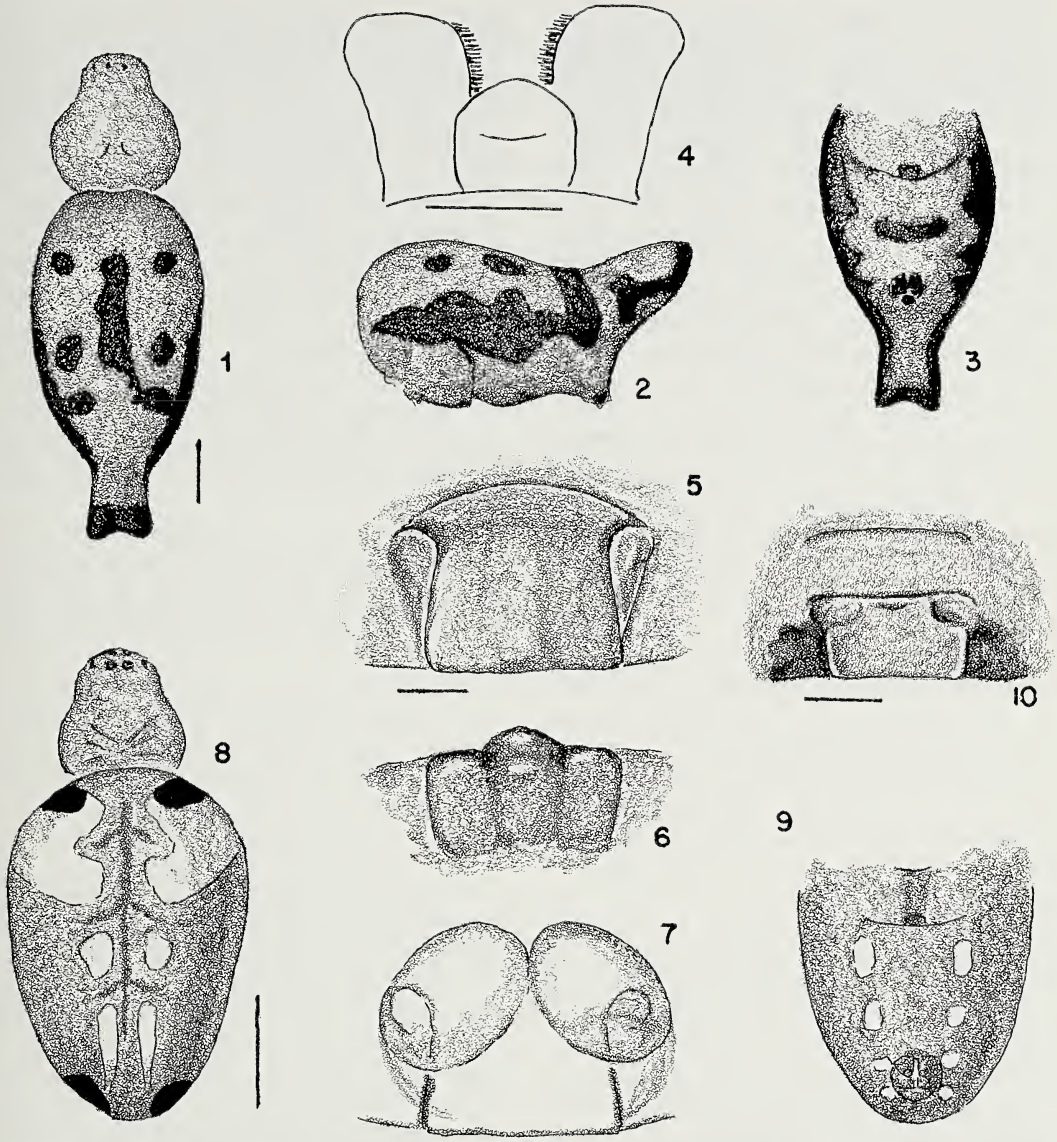
Alcimosphenus bifurcatus: immature holotype, Port Antonio and Castleton, Jamaica (YPM), not examined.

Acusilas rufonigra: 2 female syntypes, Loma del Gato, Sierra Maestra, Cuba (IESC), examined.

Acusilas rufonigra maculata: 1 specimen, Loma del Gato, Sierra Maestra, Cuba (depository unknown), not examined.

Alcimosphenus boringuenae: female holotype, Collazo Falls, east of Sebastian, Puerto Rico (AMNH), examined.

Other specimens examined.—Specimens from Cuba, Hispaniola, Jamaica, Puerto Rico, St Croix and Montserrat were examined. Si-



Figures. 1–10.—*Alcimosphenus licinus* Simon. 1. Carapace and abdomen, dorsal; 2. Abdomen, lateral; 3. Abdomen, ventral; 4. Labium and endites; 5–7. Epigynum; 5. Ventral; 6. Posterior; 7. Ventral, cleared. 8–10. *Leucauge rubripleurus* (Mello-Leitão). 8. Carapace and abdomen, dorsal; 9. Abdomen, ventral; 10. Epigynum, ventral. Scale lines, 1.0 mm; of genitalia 0.1 mm; Fig. 4 = 0.5 mm.

mon (1897) recorded this species from St Vincent and Trinidad.

Description.—*Female (syntype of A. licinus from Jamaica):* Carapace orange, chelicerae, labium, endites, sternum, coxae orange. Legs black. Abdomen orange with black patches (Figs. 1–3). Carapace flat with two curved thoracic grooves (Fig. 1). Labium wider than long, with large lip, endites longer than wide, distally swollen, much wider than at base (Fig. 4). Posterior eye row straight. Eyes small and subequal. Lateral eyes adjacent to each other. Total length 9 mm. Carapace 2.6 mm long, 2.5 wide in thoracic region, 1.5 wide in cephalic area. First femur 3.3 mm, patella and tibia 4.1, metatarsus 3.5, tarsus 1.2. Second patella and tibia 3.3 mm, third 1.8. Fourth femur 3.6 mm, patella and tibia 3.0, metatarsus 2.8, tarsus 1.0.

Variation.—The size of adult females is 6–

10 mm total length. The illustrations were made from a female syntype of *A. licinus* from Jamaica, Fig. 7 from several non-type specimens. The internal genitalia are lightly sclerotized and no structures are distinctly visible.

The forked tail (Figs. 1, 3) is found in Jamaica specimens, although some from Jamaica have a pointed tail. Puerto Rican specimens available have a median groove at the tip. One immature specimen from Cuba had a forked tail and one small specimen from Jamaica had the tips facing in opposite directions.

The most marked specimens, with dorsal, lateral and ventral marks came from Jamaica; those from other islands generally had lateral black patches and black tail but lacked dorsal and ventral marks. The Cuban syntypes of *A. rufoniger* have a dorsal black patch on the abdomen. The Puerto Rican specimens have a wider abdomen and shorter tail and appeared better fed.

The differences in epigynal proportions between specimens with forked and pointed tails reported by Archer were not found, but Puerto Rican specimens had the sides of the epigynum slightly shorter in length than in specimens from other islands. Unlike other tetragnathids, the spermathecae are not sclerotized and are indistinct in the cleared epigynum (Fig. 7).

Relationships.—The shape of carapace (Fig. 1) and that of the abdomen (Figs. 1–3) and the rows of trichobothria on the fourth femur suggests a close relationship with *Leucauge*.

Note.—*Acusilas rufonigra maculata* differs by the black pattern on the abdomen. Franganillo Balboa does not report on this form again in his more comprehensive paper on Cuban spiders (Franganillo Balboa 1936).

Genus *Leucauge* White 1841
Leucauge rubripleurus (Mello-Leitão 1947)
NEW COMBINATION
Figs. 8–10

Alcimosphenus rubripleura Mello-Leitão 1947:239, figs. 6, 7.

Type specimens.—Female lectotype (here designated), two female paralectotypes, Rio de Areia, Paraná, Brazil (MHNC, no. 2521–2523), examined. A lectotype was designated because the epigyna of the syntypes differed slightly.

Description.—*Female (lectotype):* Carapace and chelicerae light yellow. Labium and endites gray, sternum grayish orange-brown. Legs yellowish with distal ends of femora gray. Abdomen gray with two pairs of black patches and patches of silver dorsally (Fig. 8) and ventrally (Fig. 9). The gray areas are presumed to have been red when described by Mello-Leitão (1947).

Posterior median eyes slightly larger than others, which are subequal. Anterior median eyes 0.9 diameters apart, 1.3 diameters from laterals. Posterior eyes 0.9 diameters apart, 1.2 from laterals. Total length 5.2 mm. Carapace 1.7 mm long, 1.7 wide. First femur 3.9 mm, patella and tibia 4.5, metatarsus 3.4, tarsus 1.1. Second patella and tibia 3.2 mm, third, 1.4, fourth 2.2.

This species has an epigynum that is superficially similar to that of *Alcimosphenus licinus* (Fig. 10). The preserved specimen has gray, silver and black markings on the abdomen.

It is placed here in *Leucauge* because it lacks the *Alcimosphenus* tail and the abdomen appears similar to that of other *Leucauge* species (Figs. 8, 9); also the legs are relatively longer than those of *Alcimosphenus*.

ACKNOWLEDGMENTS

Brian Farrell suggested that I check on the specific name of *Alcimosphenus*. The museum specimens were made available for study by L.F. de Armas, Havana; Bittencourt, S. de Fátima Caron, Curitiba; the late W.J. Gertsch and J.A.L. Cooke, New York; C. Rollard, Paris. Lorna Levi and Laura Leibensperger reworded parts of the manuscript. I also thank the editor, and the reviewers G. Hormiga, and N. Scharff for their helpful comments.

LITERATURE CITED

Archer, A.F. 1951. Studies in the orbweaving spiders (Argiopidae) 1. American Museum Novitates 1487:1–52.

Archer, A.F. 1958. Studies in the orbweaving spiders (Argiopidae) 4. American Museum Novitates 1922:1–21.

Archer, A.F. 1965. Nuevos Argiopidos (Arañas) de las Antillas. Caribbean Journal of Science 5: 129–133.

Franganillo Balboa, P. 1930. Arácnidos de Cuba. Instituto Nacional de Investigaciones científicas. Habana 1:47–99.

Franganillo Balboa, P. 1936. Los Arácnidos de Cuba Hasta 1936. La Habana, 183 pp.

Griswold, C.E., J.A., Coddington, G. Hormiga &

N. Scharff. 1998. Phylogeny of the orb-web building spiders (Araneae, Orbiculariae: Deinopoidea, Araneoidea). Zoological Journal of the Linnean Society 123:1–99.

Hormiga, G., W.G. Eberhard & J.A. Coddington. 1995. Web-construction behaviour in Australian *Phonognatha* and phylogeny of nephiline and the tetragnathid spiders (Araneae: Tetragnathidae). Australian Journal of Zoology 43:313–364

Mello-Leitão, C.F. de 1947. Aranhas do Paraná e Santa Catarina das Coleções do Museu Paranaense. Arquivos do Museu Paranaense 6:231–304.

Petrunkevitch, A. 1910. Some new or little known American spiders. Annals of the New York Academy of Sciences 19:205–224.

Petrunkevitch, A. 1930. The spiders of Porto Rico. Transactions of the Connecticut Academy of Arts and Sciences 30:1–355.

Platnick, N.I. 2004. The World Spider Catalog, Version 5.0. American Museum of Natural History, on line at http://research.amnh.org/entomology/spiders/catalog/index.html

Roewer, C.F. 1942. Katalog der Araneae von 1758 bis 1940. Vol. 1. Kommissions-Verlag von "Natura", Bremen.

Simon, E. 1895. Histoire Naturelle des Araignées. Vol. 1, fasc. 4, Pp. 761–1084. Libraire Encyclopédique de Roret, Paris.

Simon, E. 1897. On the spiders of the Island of St. Vincent. Proceedings of the Zoological Society of London 1897:860–890.

Manuscript received 16 March 2004, revised 24 August 2004.

2005. The Journal of Arachnology 33:758–766

DEVELOPMENT AND LIFE TABLES OF *LOXOSCELES INTERMEDIA* MELLO-LEITÃO 1934 (ARANEAE, SICARIIDAE)

Marta L. Fischer: Departamento de Biologia, CCBS, Pontifícia Universidade Católica do Paraná. Núcleo de Estudos do Comportamento Animal. Av. Silva Jardim, 1664/1101-CEP 80250-200-Curitiba, Paraná, Brazil. E-mail: marta.fischer@pucpr.br

João Vasconcellos-Neto: Departamento de Zoologia, Instituto de Biologia—Universidade Estadual de Campinas—UNICAMP—C.P. 6109—Campinas, São Paulo, Brazil. CEP 13083-970, Brasil.

ABSTRACT. *Loxosceles intermedia* is a medically important species that is abundant in Curitiba, Paraná State, Brazil. Knowledge of the postembryonic development of this species is fundamental for preventing bites by this species and for controlling its population size. In this report, postembryonic development (n = 212 spiderlings) was studied in the laboratory under ambient conditions of temperature and humidity with a standardized diet. The average duration of development (from emergence from the egg sac to maturity) was 356 ± 33 days (n = 189; range = 213–455). Spiders matured after 5th–8th molt, although most individuals matured after 7th molt. The sex ratio was 1:1. The mortality in the laboratory was low, most pronounced in the 4th and 5th instars and was associated mainly with molting. The longevity of females (1176 ± 478 days) was significantly longer than it was for males (557 ± 88.6 days). The abundance of *L. intermedia* in Curitiba, city in the southern part of Brazil, is related to aspects of its life cycle, since a slow growth, low mortality, and greater longevity enhance the reproductive potential of the species.

Keywords: Loxoscelism, life cycle, ontogeny, longevity

The genus *Loxosceles* consists of venomous species of medical importance that are widely distributed through different parts of the world. The venom of these species, which contains powerful cytotoxins, necrotoxins and hemotoxins (Gertsch 1967), together with the tendency of many species to form large populations in urban areas, close to human constructions, has made these spiders a public health problem in Chile (Schenone et al. 1970: *L. laeta* (Nicolet 1849)) and in the city of Curitiba, a city in the southern part of Brazil and capital state of Paraná (Ribeiro et al. 1993: *L. intermedia* and *L. laeta*). Knowledge of the postembryonic development of this species is fundamental in management programs to minimize bites by these spiders and to control their population size. Postembryonic development has been described for *L. laeta* (Galiano 1967; Galiano & Hall 1973), *L. reclusa* Gertsch & Mulaik 1940 (Hite et al. 1966; Horner & Stewart 1967), *L. gaucho* Gertsch 1967 (Rinaldi et al. 1997) and *L. hirsuta* Mello-Leitão 1931 (Fischer & Marques da Silva 2001). Bücherl (1961) provided some data on the nymphal period of *L. rufipes* (Lucas 1834) and *L. rufescens* (Dufour 1820) which, according to Gertsch (1967), are *L. laeta* and *L. gaucho*, respectively. Lowrie (1980, 1987) studied the influence of diet on the development of *L. laeta*. The number of molts required to reach maturity can vary within a species due to endogenous and exogenous factors, however it is waited that there is relationship with final body size (Foelix 1996). The maturation also may be correlated to the reproductive system in which the species is inserted as haplogynae and entelegynae spiders (Schneider 1997). In the same way, the difference between males and females in the use of resource of energy can be due the ecological role of each sex (Gary 2001).

In Brazil, cases of loxoscelism are frequent in the south and southeast of the country, especially in the state of Paraná. The city of Curitiba registers the largest number of spider bites by *Loxosceles*, with hundreds of bites each year. Two species, *L. intermedia* and *L. laeta* are found in the urban area. *Loxosceles intermedia*, found in the south and southeast

of Brazil, is abundant and is more common than *L. laeta*, the more cosmopolitan species (90% and 10% of occurrences in Curitiba, respectively) (Fischer 1994). This distribution raises the question about what factors favor an increase in the population size of the predominant species. In this study, we examined the postembryonic development and longevity of *L. intermedia* fed a standardized diet under ambient conditions of temperature and humidity.

The ontogeny of spiders is divided into three main periods: embryonic (egg fertilized until the establishment in the shape of spider body), larval (prelarva and larva unable to feed) and nympho-imaginal (nymphs or juveniles self-sufficient). Postembryonic development within the egg sac begins with rupture of the chorion (hatching) and ends with the first nymphal molt, after which the spiderlings emerge from the egg sac (Foelix 1996). The terminology used, based on Foelix (1996), was the following:

Within egg sac → emergence from egg sac

Fertilization
Eggs hatch by opening of egg membranes
Immobile stages (=1st instar)
First true molt to 2nd instar

Emerge as 2nd instar (mobile stage)

→ instars or nymphal instars → adult

series of molts

Sexual maturity

For this study, we use the term "instar" as each stage between molts, starting with the first instar, which, along with the first true molt, occurs inside the egg sac. Maturity is reported both as time from oviposition (egg sac construction) to the maturing molt and also as emergence from the egg sac to maturing molt. In addition, we report on a measure of growth ratio, which in this study is defined as the size of a structure divided by its size in the preceding instar.

METHODS

Postembryonic development.—The spiders studied (n = 212) were from four egg sacs built by spiders in the laboratory. The spiderlings were reared and maintained until death. The females (n = 4) from which the spiderlings were obtained had already been inseminated when collected in houses at different locations in Curitiba (lat. 25°25′48″S and long. 49°16′15″W). The spiders were collected in March and June of 1994.

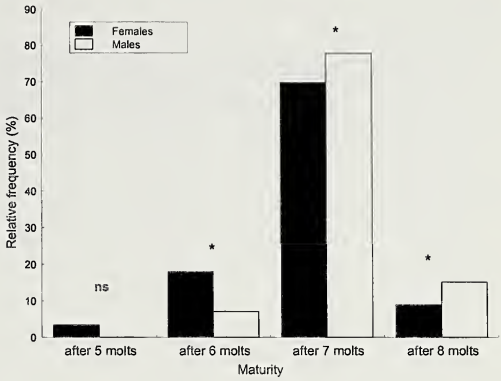


Figure 1.—Relative frequency of *Loxosceles intermedia* females and males reaching maturity after the 5th, 6th, 7th, and 8th molts. The female and male frequencies were compared using *G-test*. * = $P <$ 0.05; ns = not significant.

Following their emergence from the egg sac, the spiderlings were housed individually in 120 ml plastic containers (diameter of base 4.8 cm) and, from the 4th instar onwards, were maintained in 350 ml plastic containers (diameter of base, 6 cm), before finally being transferred to 750 ml plastic containers (diameter of base, 8 cm) at adult. All containers were lined with a double sheet of paper, which provided a substratum for locomotion, web fixation, refuge, attachment, and ecdysis. The spiders were maintained under ambient conditions of temperature, humidity, and luminosity. The air temperature and relative humidity were monitored daily using a hydrothermograph. During the study, the monthly average temperature was 21.4 ± 2.3 °C (n = 19; range = 16.2–24.7), and the average monthly humidity was 73.9 ± 11.4% (n = 19; range= 57.8–95.7). Moistened cotton was supplied weekly. Juveniles up to the 4th instar were fed a standardized diet consisting of larval and adult *Drosophila melanogaster*. After the 4th instar the spiderlings were fed *Tenebrio molitor* larvae. Two fruit flies or two mealworm larvae were supplied twice a week.

The exuvia from the molt to the 2nd instar from four egg sacs were kept dry and were measured using an ocular micrometer. Fourteen exuvia (from first molt) and 20 exuvia from the 2nd to the 8th molt (10 females and

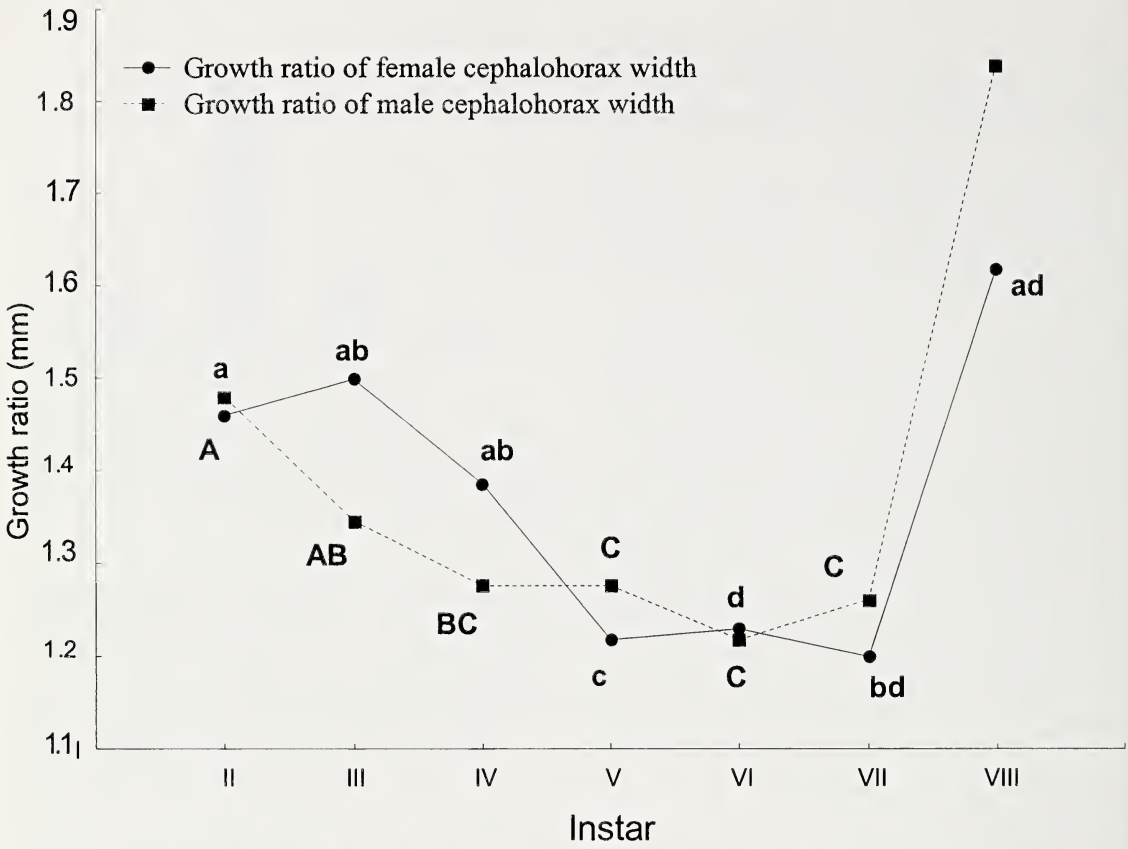


Figure 2.—Growth ratio of the cephalothorax width in successive instars of *Loxosceles intermedia* male and female (e.g., value of carapace width for instar III/ value for carapace width for instar II). The average ratios for each instar were compared using the Mann-Whitney U test. The letters (lowercase for females and uppercase for males) indicate significantly different averages ($P < 0.05$).

10 males) were examined. The sequential exuvia from all but the first molt were always from the same individuals. A thin microscope slide was placed on the exuvium to obtain measurements in the same plane. Cephalothorax width was used to compare the growth ratios of instars and adults (Huxley 1924; Hangstrum 1971; Gary 2001). The length of tibia I was used as parameter for leg growth, since total length of the leg could be affected by loss of the tarsus. To compare the size of adults that reached maturity with an additional instar, and to assess whether other body structures grew differently in males and females during postembryonic development, additional parameters were measured, including the length of the femur, tibia, metatarsus and tarsus of all legs and the femur, tibia and tarsus of the palp, the width and length of the sternum and chelicerae, and the length of the cephalothorax, labium and maxilla.

In adult females, the orange coloration of the sclerotized regions of the seminal receptacles is visible with maturity. However, maturity was only confirmed after insemination. The development of the palpal organs, which are characteristic of mature males, was apparent only after maturation. The fresh weight of mature females ($n = 86$) and males ($n = 57$) was measured to the nearest 0.1 mg.

Statistical analyses.—G-tests were used to compare the maturation rates of the different instars and the sex ratios. Since the data were not normally distributed (Shapiro-Wilks W test), the non-parametric Kruskal-Wallis (H test) were used to compare the average period between successive ecdysis and the average growth ratio of the different morphological

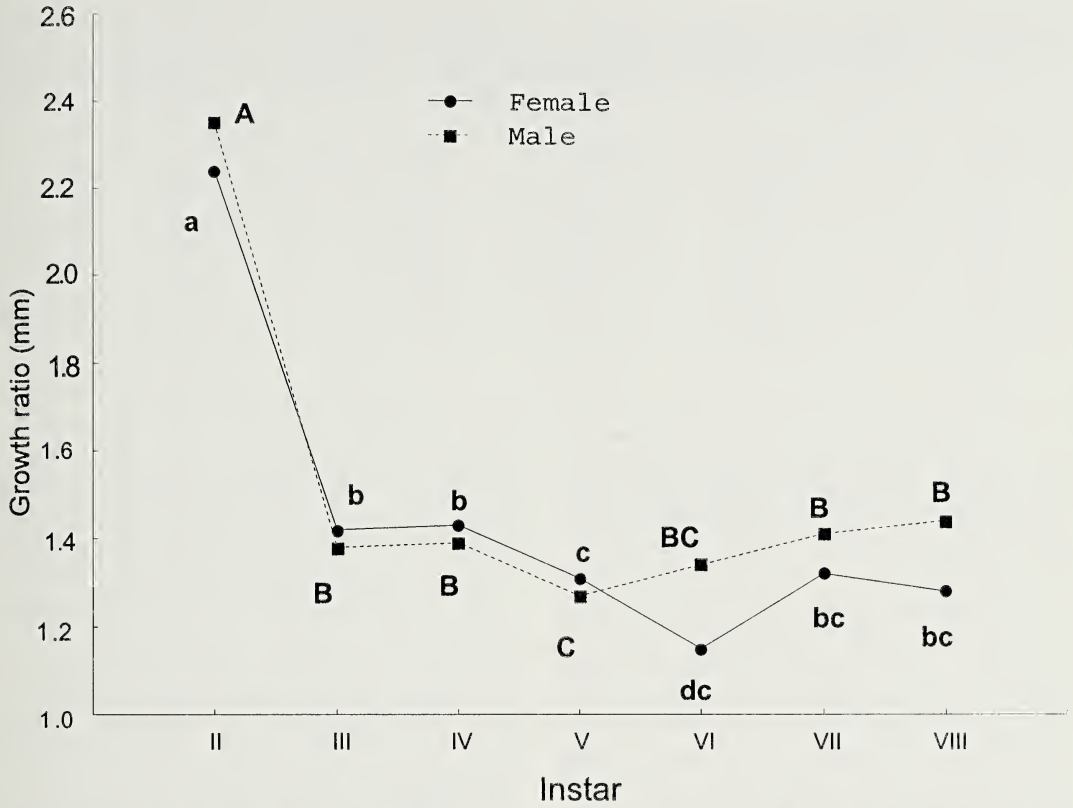


Figure 3.—Growth ratio of tibia I length in successive instars of male and female *Loxosceles intermedia* (e.g. value of tibia I length for instar III/value for tibia I length for instar II). The average ratios for each instar were compared using the Mann-Whitney U test. The letters (lowercase for females and uppercase for males) indicate significantly different averages ($P < 0.05$).

structures. The Mann-Whitney U test was used to compare the average interval between molts, the growth ratios, spider weights, and the longevity of males and females, and of spiders that reached the maturity after 7 and 8 molts.

Voucher specimens are deposited in arachnological collection Dra. Vera Regina von Eicksted in session of poisonous arthropods of Imunologic Production and Research Center (SESA-PR).

RESULTS

Number of molts and instars.—Females matured after 5–8 molts whereas males matured after 6–8 molts (Fig. 1). In both males and females, the highest frequency of maturity was after 7th molt (females: *G-test* = 44; $P < 0.001$; df = 3; males: *G-test* = 42; $P < 0.001$; df = 2). The frequency of maturation after 5th, 6th, 7th and 8th molts was different between males and females (*G-test* = 10,5; $P < 0.05$; df = 3). The highest frequency of maturity after 6th molt was observed in females, and after 7th and 8th molt in males (Fig. 1).

Duration of stages or instars.—There was no pattern of increasing or decreasing the duration of the interval between molts during development. However, the duration of the instars was different in females ($H = 380$; $P < 0.001$) and males ($H = 423.2$; $P < 0.001$) (Table 1) in the 4th to 8th instars (for 5th instar, $U = 28530.5$; $P < 0.001$; and 7th instar $U = 2215$; $P < 0.01$). The time (days) until adulthood was not significantly different between males and females ($U = 3334.5$; $P = 0.15$) (Table 2).

Growth.—A comparison of the growth ratio of the cephalothorax width showed the same pattern between males and females (Fig. 2). A growth ration of 1.5 shows that the carapace width was 1.5x greater in one instar than the previous instar. The growth ratio decreased with each instar until the VIII instar,

Table 1.—Duration (days) of *Loxosceles intermedia* nymphal instars. The different letters indicate averages that are significantly different ($P < 0.05$; Mann-Whitney U test).

	Total				Females				Males			
Instars	n	Mean ± SD	Range	U	n	Mean ± SD	Range	U	n	Mean ± SD	Range	U
II	212	41.1 ± 7.8	25–64	a	88	40.1 ± 7.6	25–64	a	101	41.5 ± 8.2	29–64	a
III	211	31 ± 6.2	14–57	b	88	31.6 ± 6.5	14–50	b	101	30.3 ± 5.4	19–57	b
IV	210	46.9 ± 22	14–198	c	88	48.1 ± 27	16–198	c	101	44.2 ± 15	14–105	a
V	200	99.5 ± 31.8	39–170	d	88	108.5 ± 32	49–167	d	101	91.3 ± 30	39–162	c
VI	192	74 ± 20	36–188	e	87	75.4 ± 21.3	36–144	e	101	73.2 ± 18.4	50–188	d
VII	164	70.1 ± 18.8	39–200	e	72	64.7 ± 13.7	39–91	f	91	72.3 ± 12.9	43–104	d
VIII	23	61.5 ± 14	45–84	f	8	60.5 ± 9.8	45–75	f	16	61.2 ± 49	45–84	e

when it increased markedly. Likewise there was no difference in the growth ratio of the tibia I length when males and females were compared (Fig. 3). The biggest change in the growth ratio of tibia I occurred between instars II and III.

The cephalothorax width did not differ among females that matured after 7th and 8th instars ($U = 20$; $P = 0.7$) (Table 3). Tibial length (II and III) increased between 7th and 8th instars ($U = 13.5$; $P < 0.01$ and $U = 16$; $P < 0.05$). In males that reached maturity after 8th instar, both the cephalothorax width ($U = 0.1$; $P < 0.001$) and tibial length of all legs (I: $U = 14$; $P < 0.01$; II: $U = 18$; $P < 0.05$; III: $U = 17.5$; $P < 0.01$; IV: $U = 9.5$; $P < 0.0001$) were significantly greater than in males that matured after the 7th instar (Table 3). The cephalothorax width did not differ between males and females that reached maturity after 7th and 8th instars. However, the tibial length was longer in males in both situations (Table 3).

The average weight of adult females was 127.4 ± 5.03 mg ($n = 86$; range = 30–240) and that of adult males was 68.6 ± 23.7 mg ($n = 57$; range = 10-=110). Females were thus significantly heavier than males ($U = 649.5$; $P < 0.001$). The weight of females that reached maturity after 7th instar was not different from that of females that reached maturity after 8th instar ($U = 163.5$; $P = 0.58$). In contrast, males that reached maturity after 8th instar were heavier than those that reached maturity after 7th instar ($U = 42$; $P < 0.01$).

Sex ratio.—Of the 212 spiderlings studied until death, 41.5% ($n = 88$) were female, 47.6% ($n = 104$) were male, and 10.8% ($n = 20$) died before reaching maturity. Of the four egg sacs studied, in two there were more males than females, but this difference was significant in only one egg sac.

Longevity.—*Loxosceles intermedia* reared in the laboratory had a low overall mortality rate. Mortality which was greatest in the 4th and 5th instars and was associated mainly with molting (immediately prior to ecdysis). The spiders sometimes remained attached to the old exoskeleton and died 1–4 days after molting. The initial instars had the greater life expectancies (ex), which then decreased during development (Table 4).

Adult longevity and total longevity post emergence was significantly greater in females than in males ($U = 589.5$; $P < 0.001$ and $U = 527$; $P < 0.001$) (Table 5). The time required for growth from oviposition to the adult stage increased with the number of ec-

Table 2.—*Loxosceles intermedia* maturation times.

	Total			Female			Male		
Time (days)	n	Mean ± SD	Range	n	Mean ± SD	Range	n	Mean ± SD	Range
Oviposition to maturity	189	409 ± 33	269–506	88	404 ± 56	112–506	101	410 ± 46	269–744
Emergence of egg sac to maturity	189	356 ± 33	213–455	88	359 ± 35.7	241–455	101	354.7 ± 31.1	258–431

Table 3.—Average tibia I length (mm) and cephalothorax width (mm) in successive instars of male and female *Loxosceles intermedia* (sample size and range in parentheses). The averages were compared using the Mann-Whitney *U* test. The letters indicate significantly different averages ($P < 0.05$).

	Tibia I		Tibia II		Tibia III		Tibia IV		Cephalothorax width	
	Mean ± SD	*U*	Mean ± SD	*U*	Mean ± SD	*U*	Mean ± SD	*U*	Mean ± SD	*U*
Male instar VII	5.9 ± 0.6 (10; 4.7–6.9)	a	7.0 ± 0.8 (10; 5.9–8.4)	a	4.8 ± 0.4 (10; 4.1–5.6)	a	5.4 ± 0.62 (10; 4.7–6.3)	a	3.0 ± 0.3 (10; 2.4–3.3)	a
Male instar VIII	6.6 ± 0.6 (10; 5.1–7.5)	b	9.3 ± 0.5 (10; 8.1–9.7)	b	5.2 ± 0.1 (10; 5–5.3)	b	6.3 ± 0.2 (10; 5.6–6.4)	b	3.8 ± 0.2 (10; 3.4–3.9)	b
Female instar VII	4.3 ± 0.7 (10; 3.1–5.3)	c	4.7 ± 0.8 (10; 3.4–5.6)	c	3.4 ± 0.6 (10; 2.3–4.4)	c	4.4 ± 0.7 (10; 3.4–5.6)	c	3.1 ± 0.3 (10; 2.5–3.6)	a
Female instar VIII	5.2 ± 0.9 (8; 4.5–6.6)	c	6.5 ± 1.8 (8; 5.2–9.4)	d	4.3 ± 0.8 (8; 3.6–5.9)	d	5 ± 0.6 (8; 4.4–5.9)	c	3.5 ± 0.45 (8; 3.1–4.4)	ab

dysis required for the spider to reach maturity (females: $H = 24.5$; $P < 0.001$ and males: $H = 31.2$; $P < 0.001$). However, the longevity as adults and the total longevity were unrelated to number of molts (Table 6).

DISCUSSION

The present study is an important reference on the basic biology of *L. intermedia*. In addition to serving as a bench mark for experimental studies, the data may be important in the preparation of management plans for the species. The observation of the 212 spiders for more than six years allowed the characterization of the postembryonic development evidencing long time to maturity, similar growth of different parts of the body in males and females, similar proportion of the sexes, little mortality and long-lived spiders in spite of their small size.

Variations in final body size of the *Loxosceles* species (Gertsch 1967) reflect the different number of molts required to reach maturity (Foelix 1996). Although the standardized number of molts in *L. intermedia* was seven, this number could be smaller or greater. The variation of up to four molts occur in *L. intermedia, L. laeta* (Galiano 1967; Lowrie 1987) and *L. gaucho* (Rinaldi et al. 1997), and the variation of only two molts in *L. hirsuta* (Fischer & Marques da Silva 2001), *L. reclusa* (Horner & Stewart 1967) and *L. rufipes* (Delgado 1966). Although *L. intermedia* has the same number of molts or more than other species, this species required more time to reach maturity (7 molts; 357 days) compared to *L. laeta* (6–9 molts; 315.3 days) (Galiano 1967) and *L. reclusa* (7 molts; 303.3) (Hite et al. 1966); *L. rufipes* (3–4 molts; 357 days) (Delgado 1966) had smaller number of molts but required the same time as *L. intermedia*.

Table 4.—Life table of *Loxosceles intermedia* reared in the laboratory (l_x = number of survivors at the start of the instar; d_x = number of deaths in the interval x and x + 1; q_x = mortality rate; e_x = average life expectancy for an individual alive at the beginning of the interval; L_x = average number of individuals alive in the interval x and x + 1; T_x = individuals for unit of time).

Instar	l_x	d_x	q_x	e_x	L_x	T_x
II	164	1	0.006	5.18	163.5	847
III	163	1	0.006	4.21	162.5	683
IV	162	10	0.006	3.32	157	521
V	152	6	0.66	2.44	149	364
VI	146	4	0.41	1.49	144	215
VII	142	142	1	1.01	71	144

The maturation period and the number of molts until maturity can vary within the same species when spiders are maintained in different conditions. In spiders, this variation is attributed to the feeding regime (Turnbull 1962, 1965; Levy 1970), temperature (Downes 1988), predation of infertile eggs by spiderlings within the egg sac (Galiano 1967; Valerio 1974) and genetic variation (Muniappan & Chada 1970; Wise 1976; Downes 1987). For *Loxosceles* the time and number of molts was attributed to the amount and composition of food (Lowrie 1980, 1987; *L. laeta*), temperature during development (Horner & Stewart 1967; *L. reclusa*) and season when the egg sac was deposited (Hite et al. 1966; *L. laeta*).

The maturation also may be correlated to the mating system, which is in turn influenced by spermathecal morphology and the pattern

Table 5.—Average longevity (days) of female and male *Loxosceles intermedia* reared in the laboratory. The values are the mean ± SD. The number of spiders and the range are shown in parentheses.

	Total	Female	Male
Longevity as adults (last molt to death)	493.7 ± 455 (175; 0–181)	816.9 ± 478.1 (83; 124–1810)	202 ± 92 (92; 0–483)
Longevity total (emergence from egg sac to death)	850.6 ± 455.8 (175; 368–2195)	1176 ± 478 (83; 465–2195)	557 ± 88.6 (92; 368–795)

of use of stored sperm (Schneider 1997). In species in which the sperm package deposited first will also be the first to leave the spermathecae (conduit spermathecae), the males should reach maturity before females, and should compete for a mate, guarding the females in order to maximize their fertilization rates. In this system (strong male-male competition) a larger body size for males is important. In *Loxosceles*, there is a single opening to the spermathecae (Gertsch 1967; Fischer 1994) and the spiders are considered haplogynae since the copulatory duct also serves as the fertilization duct (Foelix 1996). Such species are considered to have last male priority, since the sperm deposited last in the spermathecae will be the first to reach the eggs (Schneider 1997). Hence, the males reach maturity at the same time as the female, as observed in *L. intermedia* (this study) and *L. gaucho* (Rinaldi et al. 1997), or a little later, as in *L. laeta* (Galiano 1967; Galiano & Hall 1973; Lowrie 1980, 1987) and *L. hirsuta* (Fischer & Marques da Silva 2001). Experimental studies should be conducted with other *Loxosceles* to confirm this trend.

The linear growth of different parts of the body (e.g. cephalothorax width and abdomen length) means that there was no difference in the allocation of resources to specific body parts, also shown by Gary (2001) for males and females of *Linyphia triangularis* (Clerck 1757) (Linyphiidae). Although the abdomen of *L. intermedia* was not measured here, the existence of resource allocation is seen in the larger weight of the females, and the longer walking legs of the males. The female probably uses energy resources for egg production, while males have a more wandering lifestyle (mate-searching in adult life) and maximize mating with a larger number of females. On the other hand, the similar size of the cephalothorax width may indicate that there is intraspecific competition in both sexes, selecting the largest size. A larger size in females would favor a greater production of eggs, while in males a larger size would be important for competition during mating opportunities and possibly for fighting.

The long time to maturity and the similar growth of different parts of the body in males and females indicate that rapid growth mechanisms do not exist in *L. intermedia*. The rapid growth registered in *Nephila clavipes* (Linnaeus 1767) (Tetragnathidae) has ecological costs (increase in mortality) that are related to the risk of predation and parasitism (associated with increased foraging), and an inherent physiological cost because of the high food consumption (Higgins & Rankin 2001).

The lack of difference in the body size of juvenile male and female *L. intermedia* has also been observed in *L. gaucho* (Rinaldi et al. 1997) and *L. laeta* (Galiano 1967). According to Galiano (1967), instar VI was the earliest age for accurate recognition of the sexes. Again, this pattern is evidence of a similar allocation of energy resources during development in order to produce adults of similar body sizes (cephalothorax width). Although a larger size benefits both sexes, the additional molt was significant only for male *L. intermedia* and *L. hirsuta* (Fischer & Marques da Silva 2001) and reflected advantages in the accumulation of energy (Wheeler et al. 1990). In females an 8th molt probably does not influence the reproductive potential since body weight and size did not differ.

There was little mortality during development of *L. intermedia* and *L. hirsuta* (Fischer & Marques da Silva 2001). The correlation between deaths and molting (before, during or after) indicates that this is a time of great stress and a very vulnerable phase in the life history of spiders (Galiano 1967, *L. laeta*; Turnbull 1965, Agelenidae; Nuessly & Goeden 1984, Diguetidae; Downes 1993, Amaurobidae). According to Galiano (1967), the de-

Table 6.—Time (days) from emergence to adult hood, adult longevity, and longevity after emergence of female and male *L. intermedia* that reached maturity after 5th, 6th, 7th, and 8th instar. The values are the mean ± SD. The number of spiders and the range are shown in parentheses. The averages were compared using the Mann-Whitney *U* test. The letters indicate significantly different averages ($P < 0.05$).

	Females			Males		
Instar	Time to maturity	Adult longevity	Total longevity	Time to maturity	Adult longevity	Total longevity
V	258 ± 24 (4; 241–275) a	321 ± 68 (4; 273–369) a	579 ± 43.8 (4; 548–610) a	—	—	—
VI	334 ± 42.2 (16; 263–192) b	1045 ± 400 (16; 128–1577) ab	1385 ± 396 (16; 465–1894) ab	306 ± 39.7 (7; 261–367) a	242 ± 120 (7; 146–461) a	547 ± 100 (7; 45–729) a
VII	365.3 ± 27 (62; 271–435) c	779 ± 482 (62; 124–1810) ac	1143 ± 482 (62; 495–2195) b	354 ± 23.5 (77; 258–403) b	199 ± 91 (77; 2–483) a	554 ± 88 (77; 368–795) a
VIII	382.4 ± 14.3 (8; 363–405) d	825 ± 520 (8; 18–1558) a	1204 ± 511 (8; 568–1935) ab	387 ± 22.6 (15; 331–431) c	197 ± 89 (15; 0–293) a	585 ± 91 (15; 368–705) a

lay in growth and the difficulty in molting results from an increase in the time between successive feedings. Higgins & Rankin (2001) observed that spiders fed large amounts of food were more likely to die at or immediately before the next molt.

The abundance of *L. intermedia* in Curitiba is associated with aspects of this species' life cycle. The long period until maturity is reached results in large body size and a low mortality rate. The fertilization of a larger number of females by males is favored by the greater longevity and larger body of the males. Likewise, the life span of up to five years in adult females maximizes their reproductive potential by allowing than to be fertilized by successive generations of males.

ACKNOWLEDGMENTS

The authors thank Prof. Dr. Luís Amilton Foerster, Dra. Sylvia Lucas and Dra. Gail Stratton for their comments and help in preparing this manuscript and Liliani Tiepolo and Claudia Staudacher for supplying the females of *L. intermedia*. This paper was suported by Curso de Pós-Graduação em Zoologia—Universidade Federal do Paraná—UFPR and CAPES. J. Vasconcellos-Neto was supported by a grant from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, grant no. 300539/94-0) and BIOTA/FAPESP—The Biodiversity Virtual Institute Program (grant no. 99/05446-8).

LITERATURE CITED

Bücherl, W. 1961. Aranhas do gênero *Loxosceles* e loxoscelismo na América. Ciência e Cultura 13: 213–224.

Delgado, A. 1966. Investigación ecológica sobre *Loxosceles rufipes* (Lucas), 1834 en la región costera del Perú. Memórias do Instituto Butantan 33:683–688.

Downes, M.F. 1987. Postembryonic development of *Latrodectus hasselti* Thorell (Araneae: Theridiidae). Journal of Arachnology 14:293–301.

Downes, M.F. 1988. The effect of temperature on oviposition interval and early development in *Theridion rufipes* Lucas (Araneae, Theridiidae). Journal of Arachnology 16:41–45.

Downes, M.F. 1993. The life history of *Badumna candida* (Araneae; Amaurobidae). Australian Journal of Zoology 41:441–466.

Fischer, M.L. 1994. Levantamento das espécies do gênero *Loxosceles* Heinecken & Lowe, 1832 no município de Curitiba, Paraná, Brasil. Estudos de Biologia 38:65–86

Fischer, M.L. & E. Marques da Silva. 2001. Oviposição e desenvolvimento de *Loxosceles hirsuta* Mello-Leitão, 1931 (Araneae; Sicariidae). Estudos de Biologia 47:15–20.

Foelix, R.F. 1996. Biology of Spiders. 2nd ed. New York: Oxford University Press.

Galiano, M.E. 1967. Ciclo biologico e desarollo de *Loxosceles laeta* (Nicolet, 1849). Acta Zoologica Lilloana 23:431–464.

Galiano, M.E. & M. Hall. 1973. Datos adicionales sobre el ciclo vital de *Loxosceles laeta* (Nicolet) (Araneae). Physis 32:277–288.

Gary, H.P.L. 2001. Sexual size dimorphism and juvenile growth rate in *Linyphia triangularis* (Linyphiidae; Araneae). Journal of Arachnology 29: 64–71.

Gertsch, W.J. 1967. The spider genus *Loxosceles* in South America (Araneae, Scytodidae). Bulletin of the American Museum of Natural History 136:117–174.

Hangstrum, D.W. 1971. Carapace width as a tool for evaluating the rate of development of spiders in the laboratory and the field. Annals of the Entomological Society of America 64:757–760.

Higgins, L.E. & M.A Rankin. 2001. Mortality of

rapid growth in the spider *Nephila clavipes*. Functional Ecology 15:24–28.

Hite, M.J., W.J. Gladney, J.L. Lancaster J.R. & W.H. Whitcomb. 1966. Biology of the brown recluse spider. Arkansas Agriculture Experimental Station Bulletin 711:2–26.

Horner, N.V. & K.W. Stewart. 1967. Life history of the brown spider, *Loxosceles reclusa* Gertsch and Mulaik. Texas Journal of Sciences 19:333–347.

Huxley, J.S. 1924. Constant differential growth-ratio and their significance. Nature 114:895–896.

Levy, G. 1970. The life cycle of *Thomisus onustus* (Thomisidae: Araneae) and outlines for the classification of the life histories of spiders. Zoology 160:523–536.

Lowrie, D.C. 1980. Starvation longevity of *Loxosceles laeta* (Nicolet) (Araneae). Entomological News 91:130–132.

Lowrie, D.C. 1987. Effects of diet on the development of *Loxosceles laeta* (Nicolet) (Araneae, Loxoscelidae). Journal of Arachnology 15:303–308.

Muniappan, R.H. & L. Chada. 1970. Biology of the crab spider, *Misumenops celer*. Annals of the Entomology Society of America 63:1718–1722.

Nuessly, G.S. & R.D. Goeden. 1984. Aspects of the biology and ecology of *Diguetia mojavea* Gertsch (Araneae, Diguetidae). Journal of Arachnology 12:75–85.

Ribeiro, L.A, V.R. D.V. Eickstedt, G.B.G. Rubio, J.F. Konolsaisen, Z. Handar, M. Entres, V.A. F.P. Campos & M.T. Jorge. 1993. Epidemiologia do acidente por aranhas do gênero *Loxosceles* Heineken & Lowe no Estado do Paraná (Brasil). Memórias do Instituto Butantan, 55:19–26.

Rinaldi, M.P.I., L.C., Forti & A.A, Stropa. 1997. On the development of the brown spider *Loxosceles* gaucho Gertsch (Araneae, Sicariidae): the nympho-imaginal period. Revista Brasileira de Zoologia 14:697–706

Schenone, H., A. Rojas, H. Reyes, F. Villarroel & G. Suarez. 1970. Prevalence of *Loxosceles laeta* in houses in Central Chile. American Journal of Tropical Medicine and Hygiene 19:564–567

Schneider, J.M. 1997. Timing of maturation and the mating system of the spider *Stegodyphus lineatus* (Eresidae): how important is body size?. Biological Journal of the Linnean Society 60:517–525.

Turnbull, A.L. 1962. Quantitative studies of the food of *Linyphia triangularis* Clerck (Araneae; Lyniphiidae). Canadian Journal of Entomology. 91:1233–1249.

Turnbull, A.L. 1965. Effects of prey abundance on the development of the spider *Agelenopsis potteri* (Blackwall) (Araneae: Agelenidae). Canadian Journal of Entomology 97:141–147.

Valerio, C.E. 1974. Feeding on eggs by spiderlings of *Achaearanea tepidariorum* (Araneae, Theridiidae), and the significance of the quiescent instar in spiders. Journal of Arachnology 2:57–63.

Wheeler, G.S., J. P. McCafrey & J.B. Johnson. 1990. Developmental biology of *Dictyna* spp. (Araneae: Dictynidae) in the laboratory and field. American Midland Naturalist 123:124–134.

Wise, D.H. 1976. Variable rates of maturation of the spider *Neriene radiata* (*Linyphia marginata*). American Midland Naturalist 96:66–75.

Manuscript received 9 June 2003, revised 23 October 2004.

2005. The Journal of Arachnology 33:767–775

MATE CHOICE AND SEXUAL CONFLICT IN THE SIZE DIMORPHIC WATER SPIDER *ARGYRONETA AQUATICA* (ARANEAE, ARGYRONETIDAE)

Dolores Schütz[1,2] and **Michael Taborsky**[2,3]: [1]Konrad Lorenz Institut für Vergleichende Verhaltensforschung (KLIVV), Austrian Academy of Sciences, Savoyenstraße 1a, 1160 Wien, Austria; [2]Department of Behavioural Ecology, University of Bern, Wohlenstr. 50a, 3032 Hinterkappelen, Switzerland. E-mail: Michael.Taborsky@esh.unibe.ch.

ABSTRACT. *Argyroneta aquatica* is the only spider that spends its entire life under water, and is one of the few spiders in which males are larger than females. In this paper we investigated size dependent mate choice to clarify whether intersexual selection may be partly responsible for the reversed sexual size dimorphism (SSD) in *A. aquatica*. We found that females that only copulated once could produce up to six viable egg sacs, although the number of offspring decreased with each egg sac produced. Males are the more active sex in mate acquisition and females prefer large males as mating partners. However, females fled more often from males larger than their own size (SSD > 1) than from relatively smaller males (SSD < 1), although small males approached females more often than large males did. We found that males of *A. aquatica* may cannibalize females, which to our knowledge is the first account of such reversed sexual cannibalism in spiders. The extent of SSD (m > f) determined the likelihood of females being cannibalized. Apparently, avoidance behavior of females towards the preferred, large mating partners is related to the higher risk of being cannibalized. In *A. aquatica*, intersexual selection may stabilize male size at an optimum instead of directionally selecting for large body size.

Keywords: Sexual size dimorphism, SSD, sexual cannibalism

In most web-building spiders, females are larger than males (Vollrath 1980; Head 1995). Recent studies suggest that selection pressures on male locomotory ability greatly influence optimal male body size. For terrestrial spiders, small male size has often been explained by mobility advantages (Foelix 1992). In some species, males are even able to balloon, similar to young spiderlings (Foelix 1992). Recently, Moya-Larano et al. (2002) proposed, with help of a simple biomechanical model, that smaller males are favored in species in which the male must climb to reach females in high habitat patches. They argued that the constraint imposed by gravity on climbing males is a selective factor in determining male dwarfism (Moya-Larano et al. 2002). In the water spider *Argyroneta aquatica* Clerck 1757, however, males are larger than females and larger males have mobility advantages over smaller ones when moving under water (Schütz & Taborsky 2003). Since the water spider spends its entire life under water, large body size is favored in this species more in males, the more mobile sex, than in females

Mate choice and male-male competition.—There is evidence that female choice mechanisms may influence the evolution of male body size in some spiders. Elgar et al. (2000) demonstrated that females used cannibalism to choose their preferred mates in the orb-web spider *Argiope keyserlingi* Simon 1895, in which mature males are much smaller than mature females. Females that copulated with relatively smaller males delayed sexual cannibalism and prolonged the duration of copulation. Consequently, small males fertilized more eggs than large ones (Elgar et al. 2000). In the desert spider, *Agelenopsis aperta* Koch 1837, a species in which males and females are approximately the same size at maturity, heavy males were more likely to be accepted by females (Singer & Riechert 1995).

Intrasexual competition between males may also influence optimal body size in spider males. In some sheet-web spiders (Linyphi-

[3] Corresponding author.

idae), where males are larger than females, the reversed sexual size dimorphism (SSD) probably depends on strong intrasexual selection through male-male competition for mating opportunities (Lång 2001). In contrast, male dwarfism may be the result of reduced intrasexual competition (Vollrath & Parker 1997). For example in *Nephila* spp., in which males suffer a much greater mortality risk than females due to active mate search and a higher mobility, intrasexual competition between males is strongly reduced and males are much smaller than females (Vollrath & Parker 1997).

Sexual conflict.—Mating patterns are often characterized by conflicts of interest between the sexes. Such conflicts may exist over the frequency of mating or the degree of parental investment (Warner et al. 1995; Henson & Warner 1997; Schneider & Lubin 1998; Johnson 2001). Since in spiders, males do not provide parental care and females can usually fertilize more than one clutch with a single copulation, the main conflict between the sexes in spider reproduction should be about the frequency of mating (Schneider & Lubin 1998).

Both sexes are selected to prevail in this conflict (Henson & Warner 1997; Shine et al. 2000; Eberhard 2002). In spiders, males may force copulations (Schneider & Lubin 1998) or develop adaptations that prevent the sperm of rival males from fertilizing the eggs of the female (sperm competition, Schneider & Elgar 2001). Females may reduce receptivity after one mating, they may respond aggressively towards approaching males, or they may have structures that enhance their control over mating (Schneider & Lubin 1998). Sexual conflict in spiders can even result in the death of one partner, usually when a female cannibalizes a male after, during or even before mating (Andrade 1996; Schneider & Lubin 1996; Schneider & Lubin 1998; Elgar et al. 2000).

The reversed SSD in the water spider may lead to a different outcome of sexual conflict with respect to rates of mating when the water spider is compared to other spiders. Due to their relatively large size it may be easier for *A. aquatica* males to overcome resistance of the female, and female cannibalism of males may be difficult.

The study species.—*Argyroneta aquatica* (Clerck 1757) is a solitary, aquatic spider (Heinzberger 1974) distributed in northern and middle Europe, in Siberia up to 62° latitude north, and in central Asia (Crome 1951). It is active mainly during the night (Stadler 1917; Heinzberger 1974; Masumoto et al. 1998) and shows specific adaptations to the life under water. For digesting their prey, molting, copulating, depositing eggs and raising offspring, males and females separately construct air bells under water, which are usually built between water plants and fixed with spider thread to plants or stones (Wesenberg-Lund 1939; Heinzberger 1974). The abdomen and legs bear hairs that keep an air bubble around the body to help transport air from the surface down to the air bell, and to breathe under water (Ehlers 1939). Adult males were significantly larger (males: 3.8 ± 0.67 mm, females: 3.2 ± 0.29 mm, mean ± SD) and heavier (males: 0.15 ± 0.08 g, females: 0.10 ± 0.039 g) than females (data in Schütz & Taborsky 2003).

Water spiders appear to suffer from certain constraints from their life under water (Engelhardt 1989). *Argyroneta aquatica* is not a good diver as it struggles hard to compensate for buoyancy when moving under water (Schollmeyer 1913). Males are more mobile than females. They rove around more often, actively searching for females and catching their prey mainly by active hunting (Crome 1951). Females spend most of the time inside their air bell, where they also raise their broods. They are ambush predators catching prey mainly when detecting vibrations caused by prey touching the underwater net, which surrounds their air bell. Thus, males and females have different "life styles", which may select for different body sizes (Schütz & Taborsky 2003).

In a previous study we found that *A. aquatica* males (i.e. the more mobile sex) are better divers than females, as measured by the vertical diving ability in a 1000 ml glass cylinder with and without structures to grasp. It is possible that ecological constraints select for a body size that is optimal for underwater locomotion in males much more than in females. We further found that females built larger air bells than males and that air bells size correlated with body size in females, but not so in males. Thus female size may be limited by the costs of building air bells (Schütz & Taborsky 2003). In the present study, we

investigated how this unusual direction of SSD relates to mate choice and sexual conflict in *A. aquatica*. Do females choose mates according to size, and do males compete for access to females?

METHODS

Study subjects.—All spiders used for this study were wild caught animals from four adjacent populations near Vienna, Austria, or their offspring. In 1999 and 2000 we collected more than 160 water spiders (45 adult females, 35 adult males and >80 subadults) with small fishing nets and kept each adult spider isolated in a glass jar. Whole broods and smaller subadults were held in groups in small aquaria, and all spiders were fed twice a week with living *Assellus aquaticus* or *Gammarus pulex*. The prey also survived very well in the small aquaria, so that the spiders had access to ad libitum quantities of living food. For each spider, we determined the cephalothorax width as a measure of body size (see Foelix 1992; Lång 2001). After we could determine the sex of subadult spiders, we measured their cephalothorax width when they were mature. Voucher specimens (two females) have been deposited in the Natural History Museum of Berne.

Due to very dense aquatic vegetation in the field it was impossible to observe the water spiders' behavior there and to measure population parameters such as longevity of males and females, sex ratios or spider and nest densities. From continuous size monitoring of individual spiders that were born in the lab (cephalothorax width), we found that under standardized conditions, females grew faster than males. After 200 days, females were significantly heavier than males (T-test, $T = 2.226$, $P = 0.035$, $n = 13$ males and 15 females). Lab born females survived significantly longer than lab born males (T-test, $T = 2.226$, $P = 0.035$, males: 358.9 ± 72.9 days, mean ± SD, $n = 13$, females: 479.7 ± 84.6 days, $n = 15$). In the field, females and males that are born late in the season have probably two mating seasons, with females laying several clutches per season. Much about the life history of this species remains unknown because of the difficulties of studying them in their natural habitat.

Typical mating behavior.—We observed over 50 pairings of the water spider in a variety of settings in the laboratory, and from these observations have developed a general description of a "typical" mating.

Number of young produced in successive broods after one copulation.—To find out whether females need to copulate repeatedly to fertilize subsequent clutches, we took 31 females that had matured in the lab (and thus we knew they were virgins), mated them in the lab, then held the females separately in glass jars for one year, and counted all offspring in successive egg sacs.

Mate choice and male-male competition experiments.—In a mate choice experiment in the lab we studied which sex is more active in mate acquisition and whether either sex chooses particular individuals as mating partners. In a male-male competition experiment we tested whether males compete for access to females and whether sexual cannibalism occurs and depends on the direction and extent of SSD. The test females were mature and had laid three successive egg sacs without copulating in between before they were used in these experiments. They were kept in 2 liter holding tanks before and between experiments for at least three weeks to ensure that they were ready to mate at the beginning of each experiment. Each female was used in both experiments, with a different partner in each experiment. Each male was tested twice in both experiments, with at least two weeks between trials.

For both experiments, the bottom of each 10 liter tank was covered with 3cm of small gravel (grain size ≤ 2mm), and ten one-leaf plants (*Cryptocoryne* sp.) were put in a row in the front part of the tank, so that the spiders had the opportunity to build a diving bell between two plants or between one plant and the glass wall of the tank. The whole tank was videotaped, and the behavior of the spiders was recorded with a time lapse recorder so that 48 h were condensed into three h, and recorded on a 180 min video tape.

In the mate choice experiment, we tested for behavioral differences (i) between males and females, (ii) between large and small males and (iii) of males towards large and small females. In 20 replicates, half of the test females were presented first with a small male for two days and then with a large male for two days; in the other ten females the sequence was reversed. Large males were on av-

erage 4.6 ± 0.5 mm (cephalothorax width, mean ± SD, range: 4.05–5.8 mm), small males 3.5 ± 0.35 mm (range: 2.95–3.91 mm), and females 3.2 ± 0.26 mm (range: 2.71–4.24 mm). Each mate choice trial lasted for four days, in which the female was together with either of the two males for two days each.

The video recordings were analyzed in two ways: (A) Instantaneous time sampling: in the first hour and then every fourth hour of the experiment, we noted every five minutes real-time whether the male and female are together, either inside or outside of the female air bell. From this we calculated the percent of time each pair stays together during 48 hours and compared these times between large and small males. For females we also noted whether they built an egg sac. (B) Continuous recording: during the whole experimental period we continually recorded which spider approached the other, fled from the other, and which spider cannibalized the other. For each spider we calculated the frequency of approaching and fleeing within 48 hours, and compared these frequencies between (i) males and females, (ii) smaller and larger males, and (iii) males towards the larger and towards the smaller females. We also analyzed whether females fled more often or spent more time together with either of the two males. From 14 videos we could analyze the first experimental pairing of the female with a male, and from 12 of these 14 videos we were able to analyze the experimental pairing of the female also with the second male.

We noted the location of each spider twice a day (between 10.00–11.00 and between 17.00–18.00) in the mate choice experiment, whether a male and female were together, whether they showed courtship behavior (e.g., the male chasing the female outside of the bell or both spiders swimming around until they meet again in the bell) or mating behavior (i.e. copulations or when the two spiders are in an entangled position), and whether females built egg sacs. When the female courted, mated or built an egg sac only with one male, we interpreted this as "preference" for this male. When a female showed any such preference with the first male on days 1 and 2, we left her in the tank to observe encounters with the second male on days 3 and 4, and to see whether females re-mate in dependence of the relative sizes of the two partners.

In the male–male competition experiment, two differently-sized males were released in one tank on the first day and kept together for two days. For the following two days a female was added. Sixteen replicates were performed each with different individuals. The daily recordings were similar to the female choice experiments, and we analyzed whether females preferred to copulate with either of the two males.

We analyzed aggressive behavior between males and whether cannibalism (intra- and intersexual) occurred. If it happened, we analyzed whether its occurrence depended on the degree and direction of SSD. For this we pooled the data from the mate choice and male-male competition experiments. From the mate choice experiment we included the cases in this analysis in which the female was combined with the larger of the two males (n = 20). In the male-male competition experiments the females were together with two males simultaneously. We only included the SSDs between the female and the larger male in this analysis (n = 16), because due to the male-female size difference only the larger males were candidates for sexual cannibalism.

Statistics.—Data distributions were tested for normality (Kolmogorov-Smirnoff one-sample tests, $P > 0.1$). Non-parametric statistics were used if significant differences from normal distributions were found ($P < 0.1$), and when the sample size was too low to test reliably for normality. Otherwise we used parametric statistics. All tests were two-tailed.

RESULTS

Typical mating behavior.—A typical mating in *A. aquatica* starts with the male approaching the female in her living bell (see also Braun 1931). Once in the bell, the male chases the female out of the bell and both spiders swim around for a short while until they meet again in the bell, a behavior called "courtship swimming". Once they are back in the bell, the female accepts the male, they chase each other around the air bell and after a short period they start copulating. Copulation takes place in the female's living bell, where the male transfers the sperm to the female, and the spiders remain in an entangled position for some seconds. Copulations take place several times, and after the last one the pair remains together in the bell for some min-

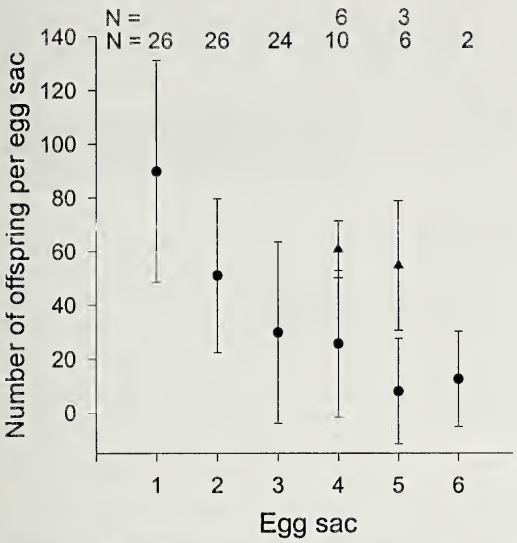


Figure 1.—Number of spiderlings per egg sac produced in successive egg sacs by *Argyroneta aquatica* without copulation between successive broods (dots) and with copulation after the third egg sac was produced (triangles, means and standard deviations).

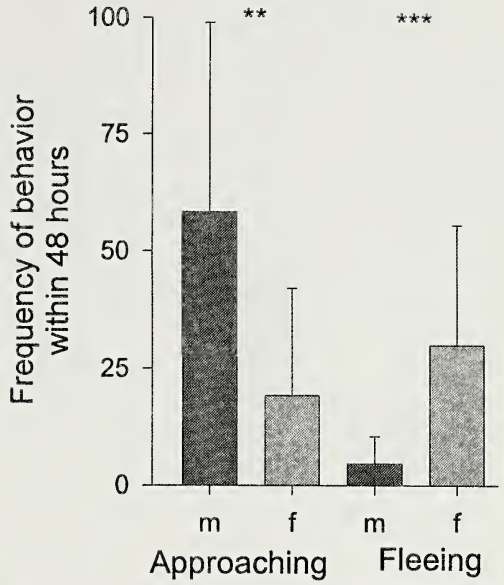


Figure 2.—Frequency of approaching and fleeing from each other in males and females during 48 hours (means and standard deviations).

utes, while the female starts building an egg sac (see also Braun 1931). Producing an egg sac took a few hours. The female cares for the brood alone (27 ± 2.61 days in the first broods of each female in this study, $n = 23$; see also Hamburger 1910; Stadler 1917; Crome 1951). When the female does not accept the male, she tries to chase the male out of her bell, but often looses the conflict by loosing her bell and sometimes even her life (see below), and then the male stays in the bell.

Number of young produced in successive broods after one copulation.—Of the 31 females that were known to have mated only once, 26 produced at least three successive egg sacs. A few females produced up to six egg sacs while they were isolated in single glass jars for a year. The number of spiderlings per egg sac decreased significantly with increasing egg sac number (Spearman correlation, $r = -0.943$, $P = 0.005$, $n = 6$, Fig. 1). A pairwise comparison of the numbers of spiderlings per egg sac in the first and second egg sacs revealed that females raised significantly more young in the first eggs sac than in the second (paired T-test, $T = 5.611$, $n = 26$ females, $P = 0.001$). Females that copulated a second time after producing the third egg sac produced significantly more offspring in the fourth egg sac (Mann-Whitney-U-test, $Z = -2.284$, $n = 6 + 10$, $P = 0.022$) and in the fifth egg sac (Mann-Whitney-U-test, $Z = -2.263$, $n = 3 + 6$, $P = 0.024$) than females that did not copulate after the third egg sac (see Fig. 1).

Mate choice and male-male competition experiments.—*(i) Differences between males and females:* In order to assure data independence, for this analysis we only included the first experimental pairing of the female with either of the two males in the mate choice experiments. Males approached females more often than vice versa (Paired t-test, $T = 3.064$, $df = 13$, $P = 0.009$, Fig. 2), and females fled more often from males than vice versa (Paired t-test, $T = -4.017$, $df = 13$, $P = 0.001$, Fig. 2).

(ii) Behavior of large and small males towards females: In the first experimental pairing of each female with a male in the mate choice experiments, small males approached the female more often than large males did (Pearson correlation, $r = -0.624$, $n = 14$, $P = 0.017$, Fig. 3).

(iii) Male behavior towards females of different sizes: We tested with pairwise comparisons whether males behaved differently towards large and small females when they were tested with differently sized partners. There

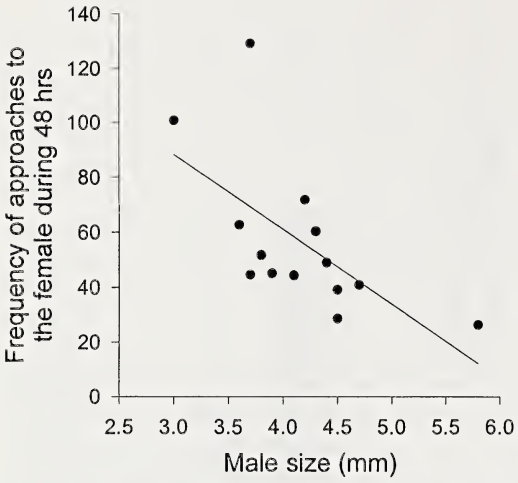


Figure 3.—Frequency of approaches of males of different sizes to the test female.

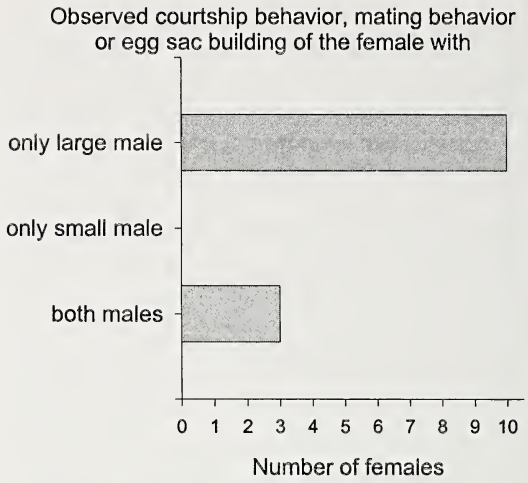


Figure 4.—Number of females courting, mating or building an egg sac with only the large male, only the small male or both males.

was no difference in the behaviors measured (Wilcoxon tests, $n = 11$, all $P > 0.15$, see methods for behaviors).

In three instances, females mated with both males. From 20 females in the mate choice experiments, 10 showed a preference because they performed reproductive behavior, i.e. courtship behavior ($n = 4$), mating behavior ($n = 3$) or egg sac building ($n = 3$) with only one of the two males. Nine females did not show a preference (Fig. 4; one female was killed during the experiment), because they performed reproductive behavior with both ($n = 3$) or with neither of the males ($n = 6$). When the test-females preferred one male, they showed reproductive activity with the larger of the two males (Binomial test, $n = 10$, $P = 0.002$), despite the fact that small males approached females more often than large males (see above). In both cases in which a female showed reproductive behavior with the smaller male first, she repeated this with the larger male, but in only one of six cases when a female showed reproductive behavior with a larger male first, did she again show reproductive behavior with the smaller male.

In the male-male competition experiment, when two differently sized males and one female were combined in one tank on days three and four, the larger male copulated with the female five times, but the smaller male never copulated with the female (Fisher's exact test, $0.05 < P < 0.1$).

In mate choice experiments with SSD > 1 (male:female, males 1.28 ± 0.13 times larger than females, $n = 22$) females fled more often from the males than in experiments with SSD < 1 (males = 0.85 ± 0.03 times female size, $n = 3$; Mann-Whitney-U-test, $Z = -2.174$, $P = 0.03$, Fig. 5). We found no significant differences in the percent of time females spent together with the larger or smaller males (Wilcoxon matched-pairs signed-ranks test, $Z = 0.0$, $n = 12$, $P = 1.0$), either inside the air bell (Wilcoxon test, $Z = -0.677$, $n = 12$, $P = 0.498$), or outside of it (Wilcoxon test, $Z = -0.7$, $n = 12$, $P = 0.944$).

Cannibalism occurred in two of 40 pairings in the mate choice experiments. In one of the 20 pairings where the female was together with the larger of the two males, the male killed the female. This was in the experiment with the highest SSD (m:f) among all experiments (SSD = 1.72:1). In the replicate in which the largest of all test females was combined with the smaller of the two males assigned to her, the female killed this male (SSD = 0.87:1). Video analysis revealed that when one spider killed another one, the killer ate the victim thereafter.

Male-male competition experiments revealed that aggression between males was very high. During the days one and two of these experiments, when two differently sized males were kept in one tank without a female, in three out of 16 experiments, aggression re-

sulted in the death of the smaller male (= 18.75%). There was no significant difference in the size disparity between the two males in cases with or without cannibalism (Mann-Whitney-U-test, $Z = -1.144$, $n = 3 + 13$, $P = 0.296$).

On days three and four of the male-male competition experiments, when two differently sized males and one female were kept in one tank, the larger male killed the female in three trials and the larger male killed the smaller male in one trial. It never happened that a female killed a male in the male-male competition experiments, or that the smaller male killed another spider.

By comparing the cases in which male cannibalism of females occurred with those in which this did not happen, the extent of SSD (m > f) was greater when cannibalism occurred (Mann-Whitney-U-test, $Z = -2.074$, $n = 4 + 22$, $P = 0.037$, see Fig. 6).

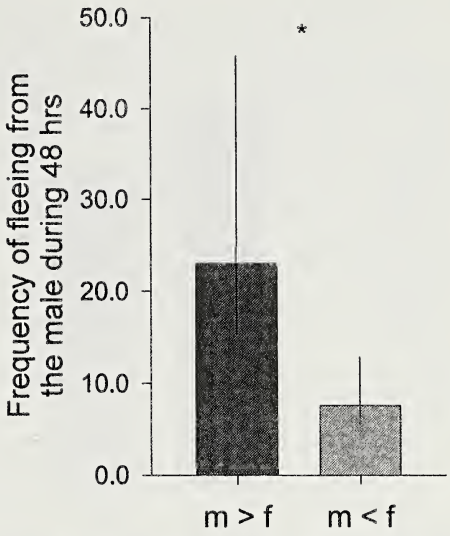


Figure 5.—Frequency of fleeing in females when the male is larger (m > f) or smaller (m < f) than the female (medians and quartiles).

DISCUSSION

Our results show that, although the number of offspring per egg sac decreased, females that only copulated once could produce up to six viable clutches. Test females that copulated a second time after producing three successive egg sacs had a higher reproductive success in their fourth and fifth clutches than females that did not copulate again. This suggests that sperm depletion occurs in females and shows that it is to the females' advantage to mate repeatedly when producing a series of clutches.

Our experiments suggest that in addition to the natural selection acting on sexual dimorphism (Schütz & Taborsky 2003), both inter- and intrasexual selection mechanisms may be involved in the evolution of large male size in *A. aquatica*. As is usual in spiders (Foelix 1992), *A. aquatica* males are more mobile and they are the more active partners in mate acquisition. In controlled experiments they approached the females more often than vice versa, and females fled from males more often than vice versa. Females chose large males preferably as mating partners. Since small males approached females more often than large males did, female preference for large males cannot be due to a lack of contact with small males. Males did not show a preference for females of a certain size.

Aggression between males was very high and sometimes resulted in the death of the smaller male. These results suggest that in males, large size is favored by intersexual and intrasexual selection mechanisms in *A. aquatica*. Males are also the better divers in this spider, so the necessity of moving under water efficiently appears to be an important determinant of large male body size as well (Schütz & Taborsky 2003).

In terrestrial spiders, often small males have locomotor advantages over larger males (e.g. see Moya-Larano et al. 2002), i.e. natural selection acts against sexual selection, which is a minor selective force in some spider species (see Vollrath & Parker 1997). Therefore, the difference in locomotor advantages of differently sized males on land and under water, together with intra- and intersexual selection mechanisms, may explain the reversed SSD of the water spider in comparison to many terrestrial spiders. In females, large size is favored by fecundity selection, but female size is apparently limited by the high costs of building air bells under water (Schütz & Taborsky 2003). This may be an additional cause of the reversed SSD in water spiders.

Sexual conflict was very obvious in our experiments and sexual contact sometimes resulted in the death of the female. To our knowledge, this reversed sexual cannibalism (i.e. males cannibalizing females) has not been reported before in any spider species. In

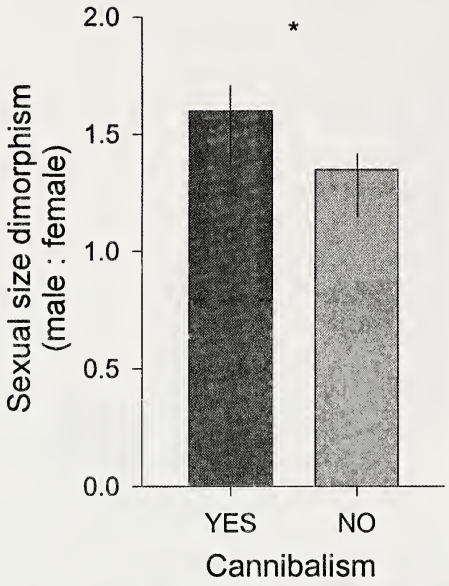


Figure 6.—Median SSDs when the male cannibalized the female and when it did not (medians and quartiles).

A. aquatica, the extent of SSD determined the likelihood of females to be cannibalized. The SSD was greater in cases when the male cannibalized the female than when he did not.

There are two main hypotheses to explain female cannibalism in spiders (see Johnson 2001; Schneider & Elgar 2002). The adaptive nutritional-advantage hypothesis postulates that sexual cannibalism is an economic, adaptive foraging strategy on the part of the adult female (Newman & Elgar 1991; Schneider & Elgar 2002). The aggressive-spillover hypothesis postulates that precopulatory sexual cannibalism is misplaced aggression favored in previous life history phases (Arnqvist & Henriksson 1997; Schneider & Elgar 2002), so it would be neutral or maladaptive. It is conceivable that these hypotheses could explain male cannibalism as well, even though the potential benefits appear to be smaller for males than for females. However, our results do not allow us to distinguish between these hypotheses for the explanation of sexual cannibalism in *A. aquatica*. In our experiments large males killed smaller females and small males, apparently dependent mainly on the direction and extent of the size difference. Sexual cannibalism in *A. aquatica* seems to follow the simple rule "Large eats Small".

An aspect of particular interest is the observed preference of females for large males, despite the risk of cannibalism. There is an apparent conflict between attraction and avoidance as females often flee from large males. Sexual cannibalism by otherwise preferred, large males might select for large female size, in addition to fecundity selection. However, female size is apparently limited by the energetically costly and risky air bell building and maintenance, which is size dependent in females but not in males (Schütz & Taborsky 2003).

In contrast to other species, mate choice in *A. aquatica* may select for an "optimal male size" instead of directional selection for large size. Usually, natural selection constrains SSD against the action of sexual selection by limiting the evolution of extreme body size in one of the two sexes. For example, a comparative study of North American passerines suggested that sexual selection for increased male size is balanced by energetic constraints of paternal care (Hughes & Hughes 1986; see also Cabana et al. 1982; Saether et al. 1986; Joensson & Alerstam 1990). In *A. aquatica* intersexual selection may stabilize male size without a necessary limitation imposed by natural selection, with sexual cannibalism being the constraining factor.

ACKNOWLEDGMENTS

We thank Thomas Drapela for his help with the experiments, and Thomas Drapela, Nicole Madlener and Katinka Maurer for their help in analyzing the videos. Karin Donnerbaum, Katharina Peer, Michaela Ritzmeier and Eva Skubic helped to collect the spiders from various field locations, and Franz Bratter helped to take care of the spiders in the lab. The project was funded by the Jubiläumsfonds der Stadt Wien für die Österreichische Akademie der Wissenschaften, project number STI 0040.

LITERATURE CITED

Andrade, M.C.B. 1996. Sexual selection for male sacrifice in the Australian redback spider. Science 271:70–72.

Arnqvist, G. & S. Henriksson. 1997. Sexual cannibalism in the fishing spider and a model for the evolution of sexual cannibalism based on genetic constraints. Evolutionary Ecology 11:255–273.

Braun, F. 1931. Beiträge zur Biologie und Atmungsphysiologie der *Argyroneta aquatica* Cl. In: Hartmann, M., R. Hesse. Zoologische Jahrbücher (Syst) 62:175–262. Jena.

Cabana, G., A. Frewin, R.H. Peters & L. Randall. 1982. The effect of sexual size dimorphism on variations in reproductive effort of birds and mammals. The American Naturalist 120:17–25.

Crome, W. 1951. Die Wasserspinne. Akademische Verlagsgesellschaft Geest & Portig K.-G., Leipzig.

Eberhard, W.G. 2002. The function of female resistance behavior: Intromission by male coercion vs. female cooperation in sepsid flies (Diptera: Sepsidae). Revista de Biologia tropical, 50:485–505.

Ehlers, M. 1939. Untersuchungen über Formen aktiver Lokomotion bei Spinnen. Zoologische Jahrbücher Systematik 72:373–499.

Elgar, M.A., J.M. Schneider & M.E. Herberstein. 2000. Female control of paternity in the sexually cannibalistic spider *Argiope keyserlingi*. Proceedings of the Royal Society London B. 267: 2439–2443.

Engelhardt, W. 1989. Was lebt in Tümpel, Bach und Weiher? Franckh'sche Verlagsbuchhandlung, Stuttgart.

Foelix, R.F. 1992. Biologie der Spinnen. Georg Thieme Verlag, Stuttgart.

Hamburger, C. 1910. Zur Anatomie und Entwicklungsgeschichte der *Argyroneta aquatica* Cl. Zeitschrift für wissenschaftliche Zoologie 96:1–31.

Henson, S.A. & R.R. Warner. 1997. Male and female alternative reproductive behaviors in fishes: A new approach using intersexual dynamics. Annual Review of Ecology and Systematics 28: 571–595.

Head, G. 1995. Selection on fecundity and variation in the degree of sexual size dimorphism among spider species (class Araneae). Evolution 49: 776–781.

Heinzberger, R. 1974. Verhaltensphysiologische Untersuchungen an *Argyronetha aquatica* Cl. PhD Thesis. Friedrich-Wilhelms-Universität zu Bonn. Wuppertal.

Hughes, A.L. & M.K. Hughes. 1986. Paternal investment and sexual size dimorphism in North American passerines. Oikos 46:171–175.

Joensson, P.E. & T. Alerstam. 1990. The adaptive significance of parental role division and sexual size dimorphism in breeding shore birds. Biological Journal of the Linnean Society 41:301–315.

Johnson, J.C. 2001. Sexual cannibalism in fishing spiders (*Dolomedes triton*): an evaluation of two explanations for female aggression towards potential mates. Animal Behaviour 6:905–914.

Lång, G.H.P. 2001. Sexual size dimorphism and juvenile growth rate in *Linyphia triangularis* (Linyphiidae, Araneae). Journal of Arachnology 29: 64–71.

Masumoto, T., T. Masumoto, M. Yoshida & Y. Nishikawa 1998. Time budget of activity in the water spider *Argyroneta aquatica* (Araneae: Argyronetidae) under rearing conditions. Acta Arachnologica 47:125–131.

Moya-Larano, J., J. Halaj & D.H. Wise. 2002. Climbing to reach females: Romeo should be small. Evolution 56:420–425.

Newman, J.A. & M.A. Elgar. 1991. Sexual cannibalism in orb-weaving spiders: an economic model. The American Naturalist 138:1372–1395.

Saether, B.E., J.A. Kaalaas, L. Loefaldi & R. Andersen. 1986. Sexual size dimorphism and reproductive ecology in relation to mating systems in waders. Biological Journal of the Linnean Society 28:273–284.

Schneider, J.M. & M.A. Elgar. 2001. Sexual cannibalism and sperm competition in the golden orb-web spider *Nephila plumipes* (Araneoidea): female and male perspectives. Behavioral Ecology 12:547–552.

Schneider, J.M. & M.A. Elgar. 2002. Sexual cannibalism in *Nephila plunipes* as a consequence of female life history strategies. Journal of Evolutionary Biology 15:84–91.

Schneider, J.M. & Y. Lubin. 1996. Infanticidal male eresid spiders. Nature 381:655–656.

Schneider, J.M. & Y. Lubin. 1998. Intersexual conflict in spiders. Oikos 83:496–506.

Schollmeyer, A. 1913. *Argyroneta aquatica*. Biologie mit besonderer Berücksichtigung der Atmung. Bruxelles, Librairie de l' Office de Publicite 6:314–338.

Schütz, D. & M. Taborsky. 2003. Adaptations to an aquatic life may be responsible for the reversed sexual size dimorphism in the water spider, *Argyroneta aquatica*. Evolutionary Ecology Research 5:105–117.

Shine, R., D. O'Connor & R.T. Mason. 2000. Sexual conflict in the snake den. Behavioural Ecology and Sociobiology 48:392–401.

Singer, F. & S.E. Riechert. 1995. Mating system and mating success of the desert spider *Agelenopsis aperta*. Behavioral Ecology and Sociobiology 36:313–322.

Stadler, H. 1917. Zur Haltung der Wasserspinnen (*Argyroneta aquatica*). Blätter für Aquarien und Terrarienkunde 28:133–136.

Vollrath, F. 1980. Why are some spider males small? A discussion including observations on *Nephila clavipes*. Verlag H. Egermann, Vienna, Austria.

Vollrath, F. & G. Parker. 1997. Giant female or dwarf male spiders? Nature 385:687.

Warner, R.R., D.Y. Shapiro, A. Marcanato, & C.W. Petersen. 1995. Sexual conflict: males with highest mating success convey the lowest fertilization benefits to females. Proceedings of the Royal Society London B. 262:135–139

Wesenberg-Lund, C. 1939. Biologie der Süßwassertiere. Springer Verlag. Wien.

Manuscript received 9 September 2003, revised 1 November 2004.

2005. The Journal of Arachnology 33:776–784

MOLECULAR INSIGHTS INTO THE BIOGEOGRAPHY AND SPECIES STATUS OF NEW ZEALAND'S ENDEMIC *LATRODECTUS* SPIDER SPECIES; *L. KATIPO* AND *L. ATRITUS* (ARANEAE, THERIDIIDAE)

James W. Griffiths[1], **Adrian M. Paterson** and **Cor J. Vink**[2,3]: Ecology & Entomology Group, PO Box 84, Lincoln University, New Zealand. E-mail: cor.vink@arachnology.org

ABSTRACT. New Zealand's endemic sand dune *Latrodectus* widow spider species, *L. katipo* and *L. atritus*, possess behavioral and physiological attributes likely to promote dispersal over large distances. Morphological, physiological and behavioral similarities between *L. katipo* and *L. hasselti*, an Australian endemic, suggest gene flow may occur across the Tasman Sea. In this study we examine intraspecific and interspecific genetic relationships within the ND1 gene region between *L. katipo*, *L. atritus*, *L. hasselti* and *L. hesperus* to assess whether the genetic evidence supports current taxonomic species designations. We found low interspecific pairwise distances among *L. katipo* and *L. atritus* populations, suggesting either introgression, incomplete lineage sorting, or that the current taxonomic distinction between the two species may be invalid. Parsimony and maximum likelihood analyses were inconclusive as to the relationships between the New Zealand *Latrodectus* species and the Australian *L. hasselti*. Low pairwise distances between *L. hasselti* and the New Zealand widow fauna indicated that *L. katipo* and *L. atritus* were not present in New Zealand before the fragmentation of Gondwana.

Keywords: *Latrodectus*, New Zealand, Australia, dispersal, molecular phylogenetics

New Zealand's endemic *Latrodectus* Walckenaer 1805 fauna is considered to comprise two endemic species, *L. katipo* Powell 1870 and *L. atritus* Urquhart 1890 (Forster & Forster 1999). *Latrodectus atritus* was originally described as a subspecies of *L. katipo* (Urquhart 1890) and was proposed as a subspecies of *L. hasselti* Thorell 1870 by Parrott (1948), and a junior synonym of *L. mactans* (Fabricius 1775) by Levi (1959). McCutcheon (1976) and Forster & Kingsford (1983) argued that *L. atritus* is a separate species to *L. katipo* and Forster (1995) elevated *L. atritus* to species but did not provide any taxonomic justification. The only reported morphological difference between *L. atritus* and *L. katipo* is coloration, which is usually unreliable for separating spider species but can be useful in separating *Latrodectus* species (McCrone & Levi 1964). *Latrodectus atritus* females do not have the red median stripe on the dorsal surface of the abdomen that *L. katipo* has (McCutcheon 1976; Forster & Kingsford 1983; Forster & Forster 1999) and the males of the two species have slight differences in color (Forster & Kingsford 1983). Forster & Kingsford (1983) also reported differences between the species in the time it took for spiderlings to emerge from the eggsac. Forster & Forster (1999) noted that *L. atritus* eggs and spiderlings need higher temperatures than *L. katipo* and they also stated that "laboratory studies show that they do not generally crossmate but when they do, the eggs are infertile" but no data was included in the publication to support this. Both New Zealand species inhabit coastal dune systems and commonly build webs in low growing plants and driftwood or flotsam. Although the niches occupied by *L. katipo* and *L. atritus* are similar, their known distributions are distinct. *Latrodectus katipo* inhabits coastal dunes in the northern half of South Island and the southern half of North Island, whereas

[1] Current address: Department of Conservation, East Coast/Hawke's Bay Conservancy, PO Box 668, Gisborne, New Zealand.
[2] Current address: Department of Biology, San Diego State University, San Diego, CA 92182–4614, USA.
[3] Corresponding author.

L. atritus inhabits coastal dunes in the northern half of North Island. There is an overlap in the species' distributions in Taranaki on the west coast of North Island (Forster & Forster 1999) and in Hawkes' Bay on the east coast North Island.

Discriminating between *Latrodectus* species using morphology has always been problematic (Levi 1983) and the distinction between *L. katipo* and the Australian *L. hasselti* is minimal. There is no difference between the male pedipalp and female external and internal genitalia of the two species (Parrott 1948; Levi 1959) but that is often the case in *Latrodectus* (Levi 1983). Forster & Forster (1999) state that the most definitive morphological character that separates the two species is the dense covering of short, fine hairs on the body of *L. katipo* compared to the long fine hairs and stouter short hairs on *L. hasselti*. *Latrodectus hasselti* females are usually larger, their webs are stronger and usually yellowish in color (Forster & Forster 1999) and this species performs a stereotyped behavior of sexual cannibalism (Forster 1992). Laboratory studies examining interspecific interactions have shown that *L. hasselti* females will not mate with *L. katipo* males (Forster 1992, 1995). However, in their phylogenetic study of *Latrodectus*, Garb et al. (2004) found that *L. katipo* and *L. hasselti* were closely related (4.9% uncorrected divergence in a 428 bp section of the mitochondrial gene cytochrome oxidase subunit I (COI)).

Recent research demonstrates that *L. katipo* and *L. atritus* are probably good dispersers. Spiderlings of both species are able to disperse by ballooning and adult females may be able to disperse on driftwood at sea under optimal conditions (Griffiths 2002). It is uncertain how far *L. katipo*, *L. atritus*, or *L. hasselti* could disperse by these means, but other ballooning spider species have been recorded landing on ships up to 300 km from land (Gertsch 1979), indicating that ballooning spiders may travel substantial distances. Furthermore, spiders recorded from driftwood and flotsam at sea, suggest that water-borne spiders could also disperse over large distances (Foelix 1996) and adult *L. hasselti* can survive more than 300 days without food (Forster & Kavale 1989). This evidence may explain why *L. katipo* and *L. atritus* distributions span numerous geographic barriers such as headlands, estuaries, rivers and areas of open sea (<30 km) and may account for morphological, physiological and molecular similarities between the New Zealand *Latrodectus* fauna and *L. hasselti*, which is considered endemic to Australia (Parrott 1948; Levi 1959; Forster & Kingsford 1983; Garb et al. 2004). As yet, however, the influence dispersal may have had on the biogeography of *L. katipo* and *L. atritus* has not been investigated. Moreover, behavioral, morphological, physiological and molecular similarities between *L. katipo* and the Australian endemic, *L. hasselti*, have not been adequately explained.

In this paper, we examine intraspecific and interspecific genetic relationships within the NADH dehydrogenase subunit 1 (ND1) mitochondrial gene region between *L. katipo*, *L. atritus*, *L. hasselti* and *L. hesperus* Chamberlin & Ivie 1935 (all part of the strongly supported "*mactans* clade" in Garb et al. 2004) to assess the degree of separation between the New Zealand and Australian *Latrodectus* species and whether genetic evidence supports current taxonomic species designations. The ND1 gene region was chosen because it is fast evolving and has been successfully used to examine genetic differences between spider species and populations (Hedin 1997a, 1997b; Masta 2000; Johannesen et al. 2002; Maddison & Hedin 2003; Masta & Maddison 2002; Vink & Paterson 2003).

METHODS

Adult female *L. katipo* and *L. atritus* were collected from eight sites around New Zealand (Fig. 1) and were stored in 95–100% EtOH at −80 °C to maintain high quality DNA. Voucher specimens are stored at the Ecology and Entomology Group, Research Collection, Lincoln University, New Zealand. Specimens were collected from sites that were selected throughout the distributions of both species. One specimen per population of *L. katipo* was collected from Kaitorete Spit (43°50′S, 172°31′E) and Waikuku Beach (43°17′S, 172°43′E), Canterbury, from Farewell Spit (40°30′S, 172°48′E), Golden Bay and from Flat Point (41°28′S, 175°37′E) and Herbertville (40°29′S, 176°37′E) on the east coast of the lower North Island (Fig. 1). One specimen per population of *L. atritus* was collected from Houpoto (37°58′S, 177°33′E), Rarawa (34°44′S, 173°05′E) and Opoutere

(37°24′S, 175°56′E) in the upper North Island (Fig. 1). *Latrodectus hasselti* were collected from Myalup, Western Australia (33°06′S, 115°41′E) and Brisbane, Queensland (27°27′S, 153°02). A specimen of *L. hesperus*, intercepted by the New Zealand Ministry of Agriculture and Forestry on table grapes from California, USA was used as an outgroup. Although *L. hesperus* is common throughout western North America (Chamberlin & Ivie 1935; Levi 1983), the identification of the *L. hesperus* specimen is tentative as a second, undescribed *Latrodectus* species is reported to be present in California (see Levi 1983) and the taxonomic differences between the two species are unknown. The entire front leg and hind leg from one side of each specimen were removed and washed in sterile deionized, distilled water to remove excess alcohol. Genomic DNA was extracted from samples using a proteinase-K digestion and high salt precipitation method (White et al. 1990). The DNA was suspended in 1:20 TE (10mM Tris, 1mM EDTA, pH 8.0).

The first half (~420 bp) of the mitochondrial ND1 gene region was amplified from diluted genomics in 25 µl PCR reactions using the primers N1-J-12261 and TL1-N-12718 (Hedin 1997a). Each 25 µl reaction contained 1× *Taq* buffer, 1 mM dNTPs, 2 µM $MgCl_2$, 0.4µM of each primer, 1.25 units *Taq* DNA polymerase (Roche), and 1µl diluted genomic DNA. Amplification took place in a GeneAmp® 2400 Thermocycler and included an initial denaturation of 4 min. at 94 °C followed by 40 cycles of 40 s at 94 °C, 40 s at 45 °C, 40 s at 72 °C and a final extension of 5 min. at 72 °C. The resulting PCR product was purified by precipitation with 50 µl of isopropanol and 25 µl NH_4Ac (2.5M) to remove excess salts and primers. Purified dsDNA samples were washed in 70% EtOH and suspended in 6 µl of sterile deionized, distilled water. All dsDNA samples were subsequently sent to the Waikato DNA Sequencing Facility where they were sequenced in both directions.

DNA sequences were aligned against a complementary-strand sequence in DNAMAN (version 4.02), and checked against hard copy chromatograms by eye. Corrections were made where necessary. The possibility of pseudogenes and polymerase errors were eliminated by the translation of the sequences to amino acids and no stop codons or frameshifts were found. A multiple alignment of all sequences was compiled in CLUSTALX (Thompson et al. 1997) and imported into PAUP* 4.0b10 (Swofford 2002) for analysis.

Data were analyzed as unordered characters using parsimony with the exhaustive option selected. Bootstrap values (Felsenstein 1985) for monophyletic groups were calculated using the branch and bound search option in PAUP*. Model test version 3.06 (Posada & Crandall 1998) was used to select the maximum likelihood parameters and the HKY + Γ model (Hasegawa et al. 1985) was used to estimate the maximum likelihood tree. The branch and bound option was selected in PAUP* for the maximum likelihood analysis and branches were collapsed creating polytomies if the branch length was ≤ 1e–08. Bootstrap values for the maximum likelihood tree were calculated using a heuristic search (10000 replicates). Base frequency calculations, transition/transversion ratios, number of variable sites and the conversion of nucleotides to amino acids were conducted using MEGA version 2.1 (Kumar et al 2001).

In addition to the molecular work, 22 specimens of *L. katipo* and *L. atritus* from collections at the Museum of New Zealand, Otago Museum, Auckland Museum and Lincoln University Entomology Research Museum were examined for differences in male and female genitalia.

RESULTS

The nucleotide composition was G (guanine) depauperate (29% A, 22% C, 10% G, 39% T), which is similar to that of the spider family Nesticidae (Hedin 1997a), a sister family of Theridiidae (Griswold et al. 1998). Sequence data were deposited in GenBank (Benson et al. 2002), accession numbers AY383604-AY383614.

The largest interspecific pairwise distance between *L. katipo*, *L. atritus* and *L. hasselti* was 1.95 %, whereas the smallest pairwise distance between the Australasian specimens and *L. hesperus* was 21.41 % (Table 2). In contrast, the largest intraspecific pairwise distance between *L. katipo* specimens was 0.97 %, which was the same as the largest pairwise distance between *L. katipo* and *L. atritus* 0.97 % and greater than the largest pairwise dis-

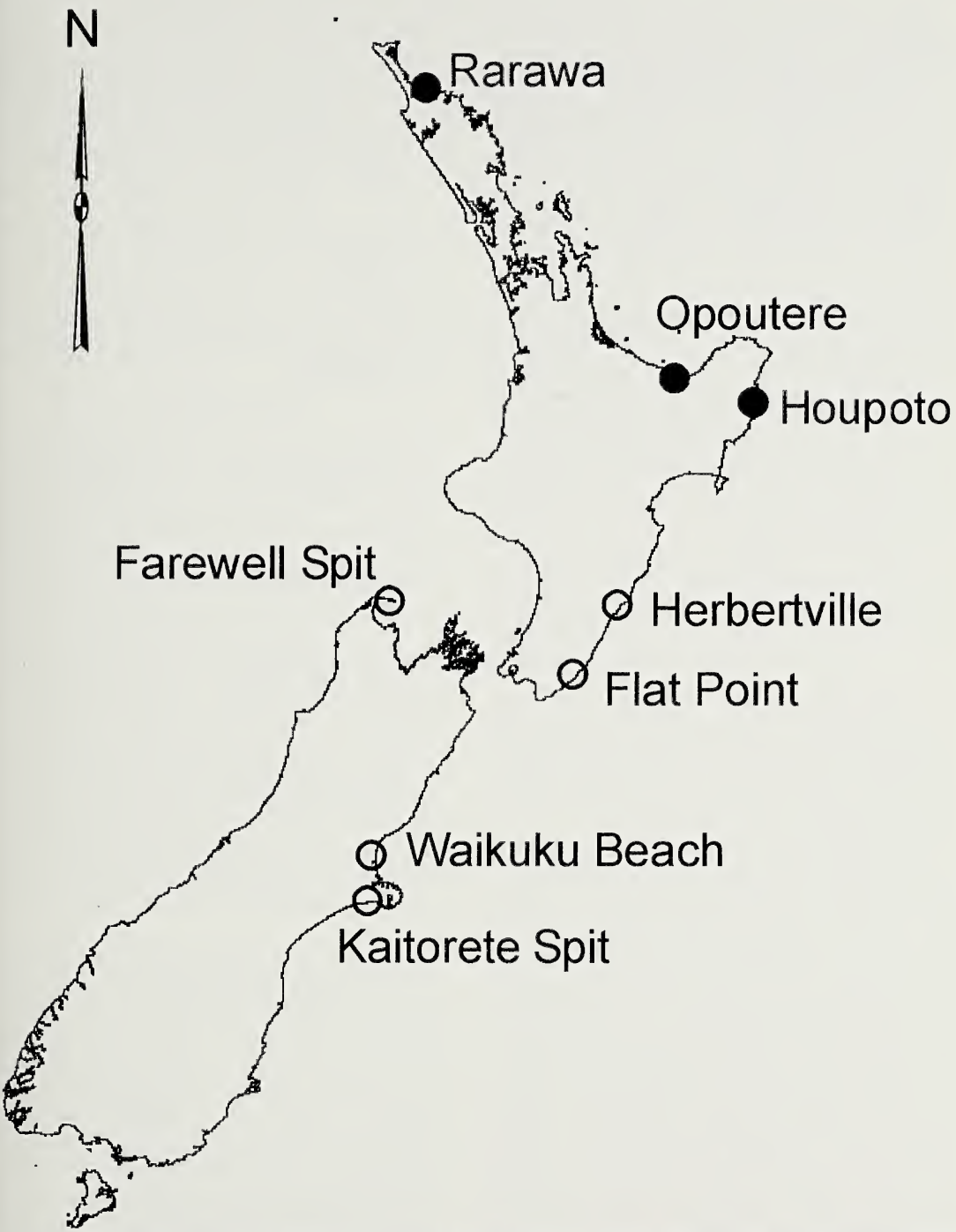


Figure 1.—Sites where *L. katipo* (○—unfilled circle) and *L. atritus* (●—filled circle) samples were collected for molecular analysis.

tance between *L. atritus* specimens 0.73 %, or *L. hasselti* specimens 0.00 % (Table 2).

Three haplotypes of *L. katipo* occurred among the specimens sampled. The *L. katipo* specimens from Herbertville and Flat Point had identical ND1 sequences as did the specimens from Farewell Spit and Wiakuku. There were three haplotypes of *L. atritus* and all

Table 1.—Base frequencies, transition/transversion ratios and number of variable sites at each codon position.

	Position 1	Position 2	Position 3
Base frequencies %	T 32.8, C 18.4, A 36.0, G 12.7	T 44.9, C 21.3, A 21.9, G 11.9	T 40.1, C 26.4, A 28.7, G 4.7
Transition/transversion ratio %	3.5	1.3	1.6
Variable sites including *L. hesperus*	16	7	68
Variable sites excluding *L. hesperus*	1	0	10

three specimens had different sequences. The ND1 sequences of both *L. hasselti* specimens were identical. Ninety-one nucleotides varied among the four *Latrodectus* species but only 11 sites varied between the *L. katipo*, *L. atritus* and *L. hasselti* specimens. Table 1 lists the base frequencies by base position, transition/transversion ratios and number of variable sites at each position.

Fourteen of the 137 amino acids coded for by the ND1 sequence were variable. Only two were variable within *L. katipo*, *L. atritus* and *L. hasselti*. There were three Australasian haplotypes. The two *L. hasselti* specimens formed one haplotype. *Latrodectus katipo* from Flat Point, Herbertville and Kiatorete Spit had identical amino acids. The third amino acid haplotype consisted of *L. katipo* from Farewell Spit and Waikuku and *L. atritus* from Houpoto, Rarawa and Opoutere.

Parsimony analysis yielded 12 equally parsimonious trees, 97 steps long with a consistency index, excluding uninformative characters, of 0.714 and a retention index of 0.714. Of the 411 characters included, 91 were variable of which four were parsimony informative. There was no consensus among the 12 trees. Maximum likelihood analysis yielded 1 tree with a score of −ln 883.451. The likelihood tree (Fig. 2) had an identical topology to one of the 12 most parsimonious trees. There was no bootstrap support for any of the clades in the parsimony analysis and only very weak bootstrap support in the maximum likelihood trees (not shown on Fig. 2); 59% for a clade containing Queensland and Western Australia, Farewell Spit and Waikuku, Houpoto, Opoutere, Rarawa, and Kiatorete Spit and 52% for the clade containing Farewell Spit and Waikuku, Houpoto, Opoutere, and Rarawa.

There were no differences in the structure of the sclerites of the male pedipalpal bulb or the sclerites of the female external epigyne of the 22 museum specimens of *L. katipo* and *L. atritus* examined.

DISCUSSION

Although too few genetic samples were collected to gain a definitive view on intra-specific gene flow between *L. katipo* and *L. atritus* populations, an indication can be inferred from the results. The maximum interspecific pairwise distance among *L. katipo* and *L. atritus* populations was 0.97%, which was smaller than most pairwise distances found in the ND1 gene region between *Nesticus* spp. populations (Hedin 1997a). Although comparisons between genera are not ideal, *Nesticus* is in a sister family to *Latrodectus* so some inference may be drawn. Low intraspecific pairwise distances among *L. katipo* and *L. atritus* populations, therefore, indicate that populations from which genetic samples were collected may not be genetically isolated or they have not yet undergone complete lineage sorting.

Both maximum likelihood and parsimony analyses revealed that these taxa were paraphyletic. In addition to this, none of the 22 museum specimens of *L. katipo* and *L. atritus* examined were found to differ in male and female genitalia. However, marked differences between *L. katipo* and *L. atritus* coloration and distribution (McCutcheon 1976; Forster & Kingsford 1983; Forster & Forster 1999) offer support for the current taxonomic designation of these species. *Latrodectus* are unusual amongst spiders in that their coloration appears to be more useful than genitalia in separating species (Levi 1983). It is possible that although *L. katipo* and *L. atritus* have not been observed mating, this does not preclude the possibility that these species may interbreed. Moreover, if color variation between the species were related to an environmental

Table 2.—Pairwise distances (uncorrected P) between ND1 sequences of *Latrodectus* spiders.

		1	2	3	4	5	6	7	8	9	10
1	*L. hasselti* (Western Australia)										
2	*L. hasselti* (Queensland, Australia)	0.0000									
3	*L. atritus* (Houpoto)	0.0170	0.0170								
4	*L. atritus* (Opoutere)	0.0195	0.0195	0.0024							
5	*L. atritus* (Rarawa)	0.0170	0.0170	0.0049	0.0073						
6	*L. katipo* (Kaitorete)	0.0146	0.0146	0.0024	0.0049	0.0073					
7	*L. katipo* (Waikuku)	0.0195	0.0195	0.0024	0.0049	0.0073	0.0049				
8	*L. katipo* (Farewell Spit)	0.0195	0.0195	0.0024	0.0049	0.0073	0.0049	0.0000			
9	*L. katipo* (Flat Point)	0.0146	0.0146	0.0073	0.0097	0.0073	0.0049	0.0097	0.0097		
10	*L. katipo* (Herbertville)	0.0146	0.0146	0.0073	0.0097	0.0070	0.0049	0.0097	0.0097	0.0000	
11	*L. hesperus* (California, USA)	0.2117	0.2117	0.21167	0.2141	0.2141	0.2093	0.2117	0.2117	0.2068	0.2068

variable, such as temperature, differences in morphology and distribution may be explained. However, we have only data from one mitochondrial gene region and the genetic differences between *L. katipo* and *L. atritus* may be due either to gene flow or incomplete lineage sorting. The validity of the species status of *L. katipo* and *L. atritus* could be further explored by the sequencing of more populations with ND1, sequencing with other mitochondrial genes (e.g., COI, which showed over three times more sequence divergence between *L. katipo* and *L. hasselti* than ND1: see Garb et al. 2004) or nuclear gene introns, the screening of microsatellites and/or detailed morphological examinations for other possible characters, especially including the mixed populations of the two species mentioned by Forster & Forster (1999). It would also be worth repeating the rearing experiments reported by Forster & Kingsford (1983) and Forster & Forster (1999) with large replicates. Until further work is undertaken *L. katipo* and *L. atritus* should be regarded as separate species.

Forster (1995) postulated that the New Zealand widow fauna had been genetically isolated from *L. hasselti* since the fragmentation of Gondwana 60–80 mya (Hayes & Ringis 1973). If Forster's (1995) hypothesis is true and *L. hasselti* and the New Zealand fauna have been isolated from one another for at least 60 my, the maximum pairwise distance (1.95%) between the *L. hasselti* and the New Zealand widow fauna suggests a rate of change the ND1 sequence of 0.0325% per million years, which is 70 times slower than mitochondrial sequence divergence reported in other arthropods (Brower 1994). Forster (1995) had also suggested that all *Latrodectus* species had a common theridiid ancestor before the break up of Pangea 400 mya (Stevens 1985), which would predate the earliest known Araneoidea fossil (Selden 1989) by 270 my and the earliest spider fossil (Shear et al. 1989) by 20 my. Much of the present day distribution of *Latrodectus* is likely to be due to dispersal events (Garb et al. 2004) and the low genetic divergence between *L. hasselti*, *L. katipo* and *L. atritus* in this study and between *L. hasselti* and *L. katipo* in Garb et al. (2004) suggests that *Latrodectus* was not present on New Zealand when it separated from Gondwana 60–80 mya. This assertion is supported

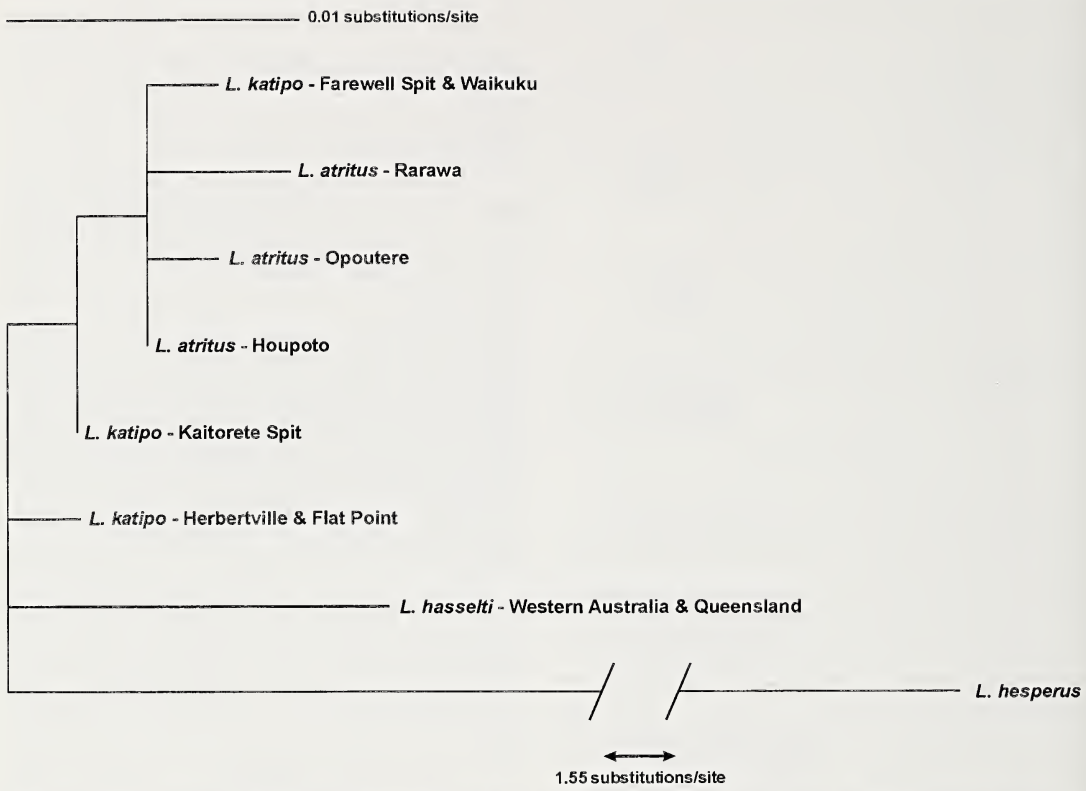


Figure 2.—Maximum likelihood tree, which has identical topology to one of the 12 equally parsimonious trees. Note the long branch of *L. hesperus*. There was not bootstrap support over 60% in the maximum likelihood analysis and none over 50% in the parsimony analysis.

by growing evidence that the New Zealand spider fauna has been, and continues to be, influenced by the arrival of spiders from Australia (Vink & Sirvid 2000; Vink et al. 2002; Vink & Paterson 2003). Given that suitable *L. katipo* and *L. atritus* habitat has probably been present in New Zealand for a long time (Stevens et al. 1988) and that the genetic evidence indicates *L. hasselti* is a good disperser, it seems unlikely that *L. katipo* and *L. atritus* are recent arrivals to New Zealand. In the absence of datable fossil records, however, it is unlikely that the time *L. katipo* and *L. atritus* arrived in New Zealand will be precisely known. Overall, this lack of evidence for isolation between Australia and New Zealand since the Gondwanan break-up agrees with other recent studies of other New Zealand taxa, such as podocarp trees (Pole 1994), galaxiid fish (Waters et al. 2000), hepialid moths (Brown et al. 1999) and various flightless insects (Trewick 2000).

It is possible some gene flow may occur, or has occurred until recently between Australian and New Zealand *Latrodectus* populations. Greater intraspecific variation found among populations of *L. katipo* or *L. atritus* than between the Australian specimens might have resulted from periods of glaciation or rising sea levels that restricted gene flow between *L. katipo* or *L. atritus* populations in New Zealand, but are unlikely to have affected *L. hasselti* (Stevens 1985; Stevens et al. 1988; Nichols 2001; Trewick 2001). Moreover, Raven (1992) and Main (1992) suggested that *L. hasselti* may have only recently been introduced to eastern Australia from South Australia, which would explain the lack of genetic variation between the *L. hasselti* specimens.

Although the ND1 mitochondrial gene region has previously been used to examine intra-specific variation between spider populations (Hedin 1997a; Hedin 1997b; Masta 2000; Johannesen et al. 2002; Maddison & Hedin 2003; Masta & Maddison 2002), this gene region did not evolve fast enough to pro-

vide the definition required to examine gene flow between populations of *L. katipo*, *L. atritus* or *L. hasselti*. Moreover, the low number of samples examined in this project also made it difficult to gain a definitive view of intraspecific gene flow. These problems might be overcome if sequence data from other faster evolving mitochondrial gene regions, such as COI (see Garb et al. 2004), or microsatellites were used and more samples were examined.

ACKNOWLEDGMENTS

Thanks to Charlie Chambers for collecting assistance. We are grateful to Ding Johnson for collecting *L. hasselti* from Western Australia, to Robert Raven (Queensland Museum) for providing *L. hasselti* from Queensland, and to David Voice (Ministry of Agriculture and Forestry) for providing the *L. hesperus* specimen. We thank Phil Sirvid (Museum of New Zealand), Brian Patrick (Otago Museum) and John Early (Auckland Museum) for the loan of specimens. This research was made possible by funding from the Department of Conservation and the Soil Plant and Ecological Sciences Division, Lincoln University.

LITERATURE CITED

Benson, D.A., I. Karsch-Mizrachi, D.J. Lipman, J. Ostell, B.A. Rapp & D.L. Wheeler. 2002. GenBank. Nucleic Acids Research 30:17–20.

Brower, A.V.Z. 1994. Rapid morphological radiation and convergence among races of the butterfly *Heliconius erato* inferred from patterns of mitochondrial DNA evolution. Proceedings of the National Academy of Sciences of the United States of America 91:6491–6495.

Brown, B., R.M. Emberson & A.M. Paterson. 1999. Phylogeny of "*Oxycanus*" lineages of hepialid moths from New Zealand inferred from sequence variation in the mtDNA COI and II gene regions. Molecular Phylogenetics and Evolution 13:463–473.

Chamberlin, R.V. & W. Ivie. 1935. The black widow spider and its varieties in the United States. Bulletin of the University of Utah 25:1–29.

Felsenstein, J. 1985. Confidence limits on phylogenies: An approach using the bootstrap. Evolution 39:783–791.

Foelix, R.F. 1996. The Biology of Spiders. Oxford University Press, New York.

Forster, L.M. 1992. The stereotyped behaviour of sexual cannibalism in *Latrodectus hasselti* Thorell (Araneae: Theridiidae), the Australian redback spider. Australian Journal of Zoology 40:1–11.

Forster, L.M. 1995. The behavioural ecology of *Latrodectus hasselti* (Thorell), the Australian redback spider (Araneae: Theridiidae): a review. Records of the Western Australian Museum Supplement 52:13–24.

Forster, R.R. & L.M. Forster. 1999. Spiders of New Zealand and their Worldwide Kin. Otago University Press, Dunedin.

Forster, L.M. & J. Kavale. 1989. Effects of food deprivation on *Latrodectus hasselti* Thorell (Araneae: Theridiidae), the Australian redback spider. New Zealand Journal of Zoology 16:401–408.

Forster, L.M. & S. Kingsford. 1983. A preliminary study of development in two *Latrodectus* species (Araneae: Theridiidae). New Zealand Entomologist 7:431–439.

Garb, J.E., A. González & R.G. Gillespie. 2004. The black widow spider genus *Latrodectus* (Araneae: Theridiidae): phylogeny, biogeography, and invasion history. Molecular Biology and Evolution 31:1127–1142.

Gertsch, W.J. 1979. American Spiders. Van Nostrand Reinhold Co, New York.

Griffiths, J.W. 2002. Web site characteristics, dispersal and species status of New Zealand's katipo spiders, *Latrodectus katipo* and *L. atritus*. Ph.D. Thesis, Lincoln University, New Zealand.

Griswold, C.E., J.A. Coddington, G. Hormiga & N. Scharff. 1998. Phylogeny of the orb-web building spiders (Araneae, Orbiculariae: Deinopoidea, Araneoidea). Zoological Journal of the Linnean Society 123:1–99.

Hasegawa, M., K. Kishino & T. Yano. 1985. Dating the human-ape splitting by a molecular clock of mitochondrial DNA. Journal of Molecular Evolution 22:160–174.

Hayes, D.E. & J. Ringis. 1973. Sea floor spreading in the Tasman Sea. Nature 243:454–458.

Hedin, M.C. 1997a. Molecular phylogenetics at the population/species interface in cave spiders of the Southern Appalachians (Araneae: Nesticidae: *Nesticus*). Molecular Biology and Evolution 14: 309–324.

Hedin, M.C. 1997b. Speciation history in a diverse clade of habitat-specialized spiders (Araneae: Nesticidae: *Nesticus*): inferences from geographic-based sampling. Evolution 51:1929–1945.

Johannesen, J., A. Hennig, B. Dommermuth & J.M. Schneider. 2002. Mitochondrial DNA distributions indicate colony propagation by single matri-lineages in the social spider *Stegodyphus dumicola* (Eresidae). Biological Journal of the Linnean Society 76:591–600.

Kumar, S., K. Tamura, I.B. Jakobsen & M. Nei. 2001. MEGA2: Molecular Evolutionary Genetics Analysis software. Bioinformatics 17:1244–1245.

Levi, H.W. 1959. The spider genus *Latrodectus*

(Araneae, Theridiidae). Transactions of the American Microscopical Society 78:7–43.

Levi, H.W. 1983. On the value of genitalic structures and coloration in separating species of widow spiders (*Latrodectus* sp.) (Arachnida: Araneae: Theridiidae). Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg 26: 195–200.

Maddison, W.P. & M.C. Hedin. 2003. Phylogeny of *Habronattus* jumping spiders (Araneae: Salticidae), with consideration of genital and courtship evolution. Systematic Entomology 28:1–21.

Main, B. 1992. Redbacks may be dinky-di after all: an early record from South Australia. Australasian Arachnology 31:3–4.

Masta, S.E. 2000. Phylogeography of the jumping spider *Habronattus pugillis* (Araneae: Salticidae): recent vicariance of sky island populations? Evolution 54:1699–1711.

Masta, S.E. & W.P. Maddison. 2002. Sexual selection driving diversification in jumping spiders. Proceedings of the National Academy of Sciences of the United States of America 99:4442–4447.

McCrone, J.D. & H.W. Levi. 1964. North American widow spiders of the *Latrodectus curacviensis* group (Araneae: Theridiidae). Psyche 71:12–27.

McCutcheon, E.R. 1976. Distribution of the katipo spiders (Araneae: Theridiidae) of New Zealand. New Zealand Entomologist 6:204.

Nichols, R. 2001. Gene trees and species trees are not the same. Trends in Ecology and Evolution 16:358–364.

Parrott, A.W. 1948. The Katipo spider of New Zealand (*Latrodectus hasseltii* Thorell). Records of the Canterbury Museum 5:161–165.

Pole, M. 1994. The New Zealand flora—entirely long-distance dispersal? Journal of Biogeography 21:625–635.

Posada, D. & K.A. Crandall. 1998. MODELTEST: testing the model of DNA substitution. Bioinformatics 14:817–818.

Raven, R.J. 1992. Redback spiders, black widows and their kin. Presidential address. News Bulletin of the Entomological Society of Queensland 20: 4–8.

Selden, P.A. 1989. Orb-web weaving spiders in the early Cretaceous. Nature 340:711–713.

Shear, W.A., J.M. Palmer, J.A. Coddington & P.M. Bonamo. 1989. A Devonian spinneret: early evidence of spiders and silk use. Science 246:479–481.

Stevens, G.R. 1985. Lands in Collision. DSIR Publishing Centre, Wellington.

Stevens, G.R., M. McGlone & B. McCulloch. 1988. Prehistoric New Zealand. Heinemann Reed, Auckland.

Swofford, D.L. 2002. PAUP*: Phylogenetic Analysis Using Parsimony (*and Other Methods), Version 4.0b10. Sinauer Associates, Sunderland, Massachusetts.

Thompson, J.D., T.J. Gibson, F. Plewniak, F. Jeanmougin & D.G. Higgins. 1997. The CLUSTAL X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acids Research 25:4876–4882.

Trewick, S.A. 2000. Molecular evidence for dispersal rather than vicariance as the origin of the flightless insect species on the Chatham Islands, New Zealand. Journal of Biogeography 27: 1189–1200.

Trewick, S.A. 2001. Scree weta phylogeography: surviving glaciation and implications for Pleistocene biogeography in New Zealand. Journal of Zoology 28:291–298.

Urquhart, A.T. 1890. Descriptions of new species of Araneidae. Transactions and Proceedings of the New Zealand Institute 22:239–266.

Vink, C.J., A.D. Mitchell & A.M. Paterson. 2002. A preliminary molecular analysis of phylogenetic relationships of Australasian wolf spider genera (Araneae, Lycosidae). Journal of Arachnology 30:227–237.

Vink, C.J. & A.M. Paterson. 2003. Combined molecular and morphological phylogenetic analyses of the New Zealand wolf spider genus *Anoteropsis* (Araneae: Lycosidae). Molecular Phylogenetics and Evolution 28:576–587.

Vink, C.J. & P.J. Sirvid. 2000. New synonymy between *Oxyopes gracilipes* (White) and *Oxyopes mundulus* L. Koch (Oxyopidae: Araneae). Memoirs of the Queensland Museum 45:637–640.

Waters, J.M., J.A. Lopez & G.P. Wallis. 2000. Molecular phylogenetics and biogeography of galaxiid fishes (Osteichthyes: Galaxiidae): dispersal, vicariance, and the position of *Lepidogalaxias salamandroides*. Systematic Biology 49:777–795.

White, T.J., T. Bruns, S. Lee & J. Taylor. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. Pp. 315–322. *In* PCR Protocols: A Guide to Methods and Applications. (M.A. Innis, D.H. Gelfand, J.J. Sninsky & T.J. White, eds.). Academic Press, San Diego.

Manuscript received 5 May 2004, revised 1 August 2004.

2005. The Journal of Arachnology 33:785–796

REVISION OF THE SPIDER GENUS *HESYDRUS* (ARANEAE, LYCOSOIDEA, TRECHALEIDAE)

James E. Carico: School of Sciences, Lynchburg College, 1501 Lakeside Drive, Lynchburg, Virginia 24501 USA. E-mail: carico@lynchburg.edu

ABSTRACT. *Hesydrus palustris* Simon and *H. habilis* (O.P.-Cambridge) are redescribed. Four new species are described: *H. caripito*, *H. yacuiba* and *H. chanchamayo* are described only from females, and *H. canar* from both male and female specimens. *Hesydrus monticola* Chamberlin is a junior synonym of *H. palustris*. *Hesydrus bucculentus* Simon is a senior synonym of *Trechalea cezariana* Mello-Leitão. *Hesydrus estebanensis* Simon is transferred to the genus *Enna* O.P.-Cambridge. *Hesydrus ornatus* Mello-Leitão and *H. bivittatus* Mello-Leitão, known only from unidentifiable spiderling holotypes, are regarded as nomina dubia. Coincidence of geographic distributions of *Hesydrus* and *Trechalea* are noted.

Keywords: New species, taxonomy, South America, Central America

This revision of the genus *Hesydrus* Simon 1898 is included in a series of studies of trechaleid genera initiated by the recognition of the validity of the family (Carico 1986) and subsequently followed by a redefinition of the family and revision of its type genus, *Trechalea* Thorell 1869 (Carico 1993). Other genera under study include *Syntrechalea* F.P.-Cambridge 1902, *Dossenus* Simon 1898, *Dyrines* Simon 1903, *Enna* O.P.-Cambridge 1897 and *Paradossenus* F.P.-Cambridge 1903, along with new genera (Carico 2005).

Members of the genus *Hesydrus* share the trechaleid habitat, which place them among rocks and around stream margins. The egg sac is a typical, flattened, bivalve disc (Carico 1993, fig. 6) which is carried on the spinnerets and provides a transportation platform for spiderlings after their emergence. Like members of the genus *Trechalea*, the egg sac is attached permanently to the spinnerets at a single location, but unlike the former, in which the attachment is in the center of the upper valve, *Hesydrus* always makes the attachment distinctly off-center.

A comparison of the distributions of species within this genus and with species of *Trechalea* reveals notable similarities throughout Central and South America. In particular, there is an apparent sympatry of particular species from each genus into comparable and identifiable geographic subregions. Therefore, the same geographic isolating mechanisms may be affecting the radiation of both genera. This is not surprising in that the habitat preferences are apparently very similar. An example is the observation that both *H. canar* new species and *T. longitarsis* (C.L. Koch 1848) are limited to the coastal river drainages of Peru, Ecuador and Colombia, while *H. palustris* Simon 1898 along with both *T. mcconnelli* Pocock 1900 and *T. paucispina* Caporiacco 1947 are found in the tributaries of the Amazon River. The common feature that separates the species cluster in the West from those in the East is the barrier afforded by the Andean continental divide. An interesting exception, however, is the occurrence of a single collection of *H. palustris* in the Canal Zone of Panama. The latter, if not due to collection mislabeling or introduction, suggests that this species has extended its range from the Pacific coastal drainages of South America into Panama. Another geographic coincidence is the occurrence of both *H. habilis* O.P.-Cambridge 1896 and *T. extensa* F.P.-Cambridge 1902 in Central America between the isthmuses of Tehuantepec and Panama which clearly suggests that the Panamanian lowlands is a barrier separating them from species in South America while Tehuantepec limits range extensions northward. The nomenclature of the genitalia and other anatomical features follow Carico (1993 [after Sierwald 1989, 1990]). The structure of both the male palpus and female genitalia in *Hesydrus* have the same basic configurations as that of *Trechalea* (Carico 1993, figs. 7–10). Because of its rigidity and resis-

tance to distortion, carapace length is emphasized as an index of body size, particularly in the discussions of variation. Measurements and figure scales are in millimeters.

Specimens examined during this study are lodged in the following museums: American Museum of Natural History, New York (AMNH); California Academy of Sciences, San Francisco (CAS); Field Museum of Natural History, Chicago (FMNH); J.E. Carico collection (JEC); Museo Argentino de Ciencias Naturales, Buenos Aires (MACN); Museum of Comparative Zoology, Harvard (MCZ); via Museu Equitoriano de Ciencias Naturales, Quito, Ecuador (MECN); Museo de la Universidad Nacional de La Plata (MLP); Museu Nacional, Universidade Federal do Rio de Janeiro (MNRJ); Muséum National d'Histoire Naturelle, Paris (MNHN); University of Costa Rica, San José (UCR); and Yale Peabody Museum, New Haven (YPM).

Since the general anatomy and color pattern within species in *Hesydrus* are quite similar, the best characters used to distinguish species are details of the genitalia. Because of the lack of representative series, it is difficult to ascertain in many cases whether some of the genitalic characters represent a range of variation within a species or indicate species-level divergence. Of particular concern is a number of singleton females representing widely divergent locations within the Amazon River basin. Although there are small, but notable, differences in the genitalic characters, I have elected to be conservative in the nomenclature for the present in light of the possibility that future collecting in the area will provide a basis for decisions. If, however, there are well-known geographic features serving as barriers between species that coincide with characters, then the latter are assumed to be of value in distinguishing species.

Transfer of *Hesydrus* species to other genera.—The apparent holotype of *Hesydrus bucculentus* Simon 1898 is a large antepenultimate male (carapace length, 7.3) of *Trechalea cezariana* Mello-Leitão 1931. *Trechalea bucculenta* (Simon 1898) is therefore a senior synonym (NEW SYNONYMY, NEW COMBINATION). This conclusion is based upon a careful anatomical examination and the consideration that the three possible Brazilian locations for the locality on the specimen label, "Thelezopolis [Theresópolis?]"

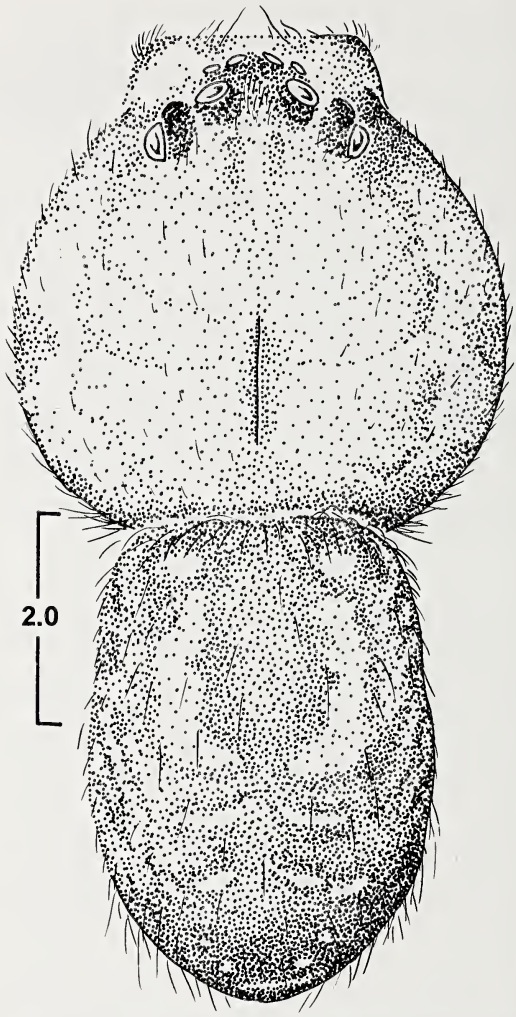


Figure 1.—Dorsal pattern of *Hesydrus palustris* male.

are at 22°25′S/42°58′W, 27°05′S/51°12′W or 30°05′S/42°58′W, all of which are within the geographical range for Simon's species. In his short description, Simon indicates the type is a female from "Brasilia" (Brazil) and the specimen examined, # 8537, has the label probably written by him.

The holotype of *H. estebanensis* Simon 1898 is actually a species of *Enna* and this species is therefore transferred to that genus [*Enna estebanensis* (Simon 1898) NEW COMBINATION]. Its taxonomic placement within the latter genus, however, is not yet determined.

Genus *Hesydrus* Simon 1898

Hesydrus Simon 1898b:305. 1898b:315 (Pisauridae); Roewer 1954:137 (Pisauridae); Bonnet

1957:2182 (Pisauridae); Lehtinen 1967:372 (transferred to Dolomedidae); Brignoli 1983:461, 465 (Dolomedidae); Carico 1986:305 (transferred to Trechaleidae); Sierwald 1990:8 ("*Trechalea* genus-group"); Carico 1993:226 (Trechaleidae); Sierwald 1993:63 (Trechaleidae); Platnick 2004 (Trechaleidae).

Type species.—*Hesydrus palustris* Simon 1898a by original designation.

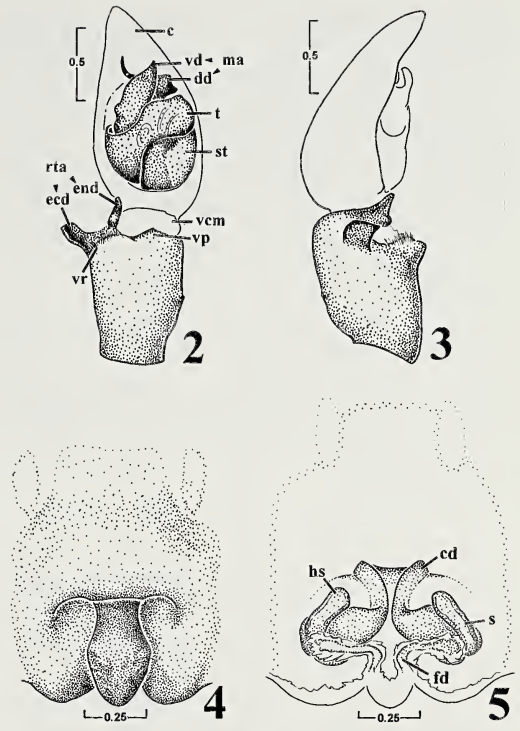
Diagnosis.—Leg I is always shorter than II and IV and approximately equal to the length of III. Both the tarsi and the distal half of the metatarsi are flexible. Chelicerae of adult males are enlarged frontally, glabrous and without distinct lateral carinae. Pairs of ventral macrosetae on the venter in all known species is: I-4, II-4, III-3 and IV-3.

Description.—Carapace moderately low, cephalic area not distinct, AE row straight or slightly recurved. Each basal segment of male chelicera swollen anteriorly and without a distinct carina: promarginal teeth three with center one largest, three retromarginal teeth sometimes with a small gap between the proximal two. Leg formula generally (IV-II)-(I-III), tarsus and distal half of metatarsi flexible, all claws dentate, paired marcosetae I-4, II-4, III-3, IV-3.

Male palpal bulb (Fig. 2) with median apophysis (ma) with distal, sickle-shaped dorsal division (dd) narrow, tapered, with tip conspicuous, and directed variably distad or laterad, the ventral division (vd) acute distally; retrolateral tibial apophysis (rta) arising distally and laterally from near the ventro-distal rim (vr) with ectal division (ecd) spatulate, and ental division (end) partly surrounded by ventral cymbio-tibial membrane (vcm); tibial (vr) of ventral protuberance (vp) folded over to create a depression in the vcm. The epigynum externally a slightly convex plate, with an elongated medial scape; internally (Fig. 5) on either side, partially attached stalked spermathecum with head (hs) slightly larger than stalk and free from other components; a single diverticulum arising from a large common chamber (probably enlarged portion of copulatory duct), both copulatory duct (cd) and fertilization duct (fd) arising from this common chamber.

Distribution.—Widespread from Guatemala southward to northern Argentina (Figs. 6, 11).

Nomina dubia.—The following two species described in *Hesydrus* are considered unidentifiable with any adult of any recognizable species:



Figures 2–5.—Genitalia of *Hesydrus palustris*. 2, 3. right palpus; 2. ventral view, 3. retrolateral view; 4, 5. female genitalia; 4. ventral view, 5. dorsal view. Apparent difference in scale in 4 & 5 is due to viewing at different tilt angles of this thick structure. (c = cymbium, cd = copulatory duct, dd = dorsal division, ecd = ectal division, end = ental division, fd = fertilization duct, hs = head of spermathecum, ma = median apophysis, rta = retrolateral tibial apophysis, s = spermathecum, t = tegulum, st = subtegulum, vcm = ventral cymbio-tibial membrane, vd = ventral division, vp = ventral protuberance, vr = ventro-distal rim.)

Hesydrus ornatus Mello-Leitão 1941. Holotype juvenile no. 14667, Yala, Jujuy, Argentina, M. Birabén, MLP, examined. The specimen is a small spiderling with a carapace length of 1.7 mm and no legs attached. There are only a few loose leg fragments but no tarsi present.

Hesydrus bivittatus Mello-Leitão 1941. Holotype juvenile no. 14666, Salta, Salta, Argentina, M. Birabén, MLP, examined. The specimen is a small spiderling with a carapace length of 1.16 mm but with all legs attached except for one.

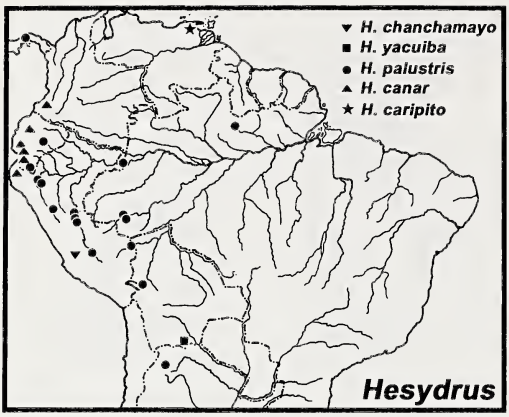


Figure 6.—Distribution of species of *Hesydrus* in South America.

Both these similar specimens are very small juveniles and are in poor condition. The legs show generalized features of lycosoids but have no specific features of *Hesydrus*. The only features that are clear enough for practical analysis are the eye pattern and what can be discerned from remnants of the dorsal pattern. The eye pattern is general for trechaleids and pisaurids, but also for the rather atypical lycosid genus, *Aglaoctenus*. In some pisaurids I have found that there may be a significant shift of the relative positions of eyes and proportions of some body parts during the transition of spiderling to adult, a significant factor to consider when identifying spiderlings in these lycosoid families. The median dorsal bands of the abdomen of both specimens are unknown in any recognized species, but then it is not unusual for spiderling coloration to be different from that of later juveniles and adults. Therefore, until a detailed comparative study can be made on juveniles of known species of these wide-ranging families, it is not possible to determine the status of these specimens. Since it is not useful to base a taxonomy on such uncertainty, I have not considered these two species further in the nomenclature of species in *Hesydrus*.

Hesydrus palustris Simon 1898
Figs. 1–6

Hesydrus palustris Simon 1898a:20; Simon 1898b: 305; F.O.P.-Cambridge 1903:165, plate 15, figs. 22–25; Roewer 1954:137; Bonnet 1957:2182; Platnick 2004.

Trechalea monticola Chamberlin 1916:276, 277, plate 23, fig. 1; Roewer 1954:143; Bonnet 1959: 4679. NEW SYNONYMY.

Hesydrus monticola (Chamberlin): Carico 1993: 237; Platnick 2004.

Type material.—*Hesydrus palustris*: lectotype male (present designation), 1 paralectotype female, Loja, Zamora, Ecuador, 4°00′S, 79°12′W, Gaujon (MNHN, examined) (Simon did not designate a holotype from the syntype series; a male lectotype is selected here to provide taxonomic stability).

Trechalea monticola: holotype, juvenile female, Santa Ana, Peru, August 1911, Yale Peruvian Expedition (MCZ, examined).

Other material examined.—ARGENTINA: *Jujuy*: "S. S." [?San Salvador de Jujuy], 24°11′S, 65°18′W, February 1966, Maury, 1 ♀ (MACN). BOLIVIA: *La Paz*: Guanay near La Paz, 16°30′S, 68°09′W, August 1989, L.E. Peña, 1 ♂, 1 ♀, 4 juveniles (AMNH). BRAZIL: *Acre*: Rio Purus NW. of Sena Madureira Seringal Santo Antônio, 9°04′S, 68°40′W, 13–18 September 1973, B. Patterson, 2 ♀ (MCZ). COLOMBIA: *Amazonas*: 35 km above Leticia, 10°22′N, 74°28′W, 15 September 1973, Mary Corn, 1 ♀ (MCZ). ECUADOR: *Pastaza*: Cusuimi, on Cusuimi River 150 km SE. Puyo, 2°43′S, 77°40′W, 15–31 May 1971, B. Malkin, 1 ♀ (FMNH). PANAMA: *Canal Zone*: Barro Colorado Island, 9°09′S, 79°50′W, 16 June–15 July 1934, A.M. Chickering, 1 ♂ (MCZ). PERU: *San Martin*: Ekin, E. of Tarapoto, 6°30′S, 76°21′W, 9–21 March 1947, F. Woytkowski, 2 ♂, 12 ♀ (AMNH); Mishqui-Yacu, 20 km NE. Moyobamba, 6°03′S, 76°58′W, 16–24 August 1947, F.Woytkowski, 2 ♀, 3 juveniles (AMNH); Hara, 20 miles SE. of Moyabamba, 6°03′S, 76°58′W, 1–30 June 1947, F. Woytkowski, 1 ♂ (AMNH); *Huanuco*: Divisoria, 9°40′S, 76°05′W, 23 September–3 October 1946, F. Woytkowski, 2 ♂, 10 ♀ (AMNH); *Loreto*: Aquaitia, 4°00′S, 75°10′W, 1–2 September 1946, F. Woytkowski, 5 ♂, 25 ♀ (AMNH); San Alejandro, 4°00′S, 75°10′W, June 1947, W. Weyrauch, 5 ♂, 2 ♀ (AMNH); *Pasco*: Upper Pachitea River, 8°46′S, 74°31′W, collector & date unknown, 1 ♀ (AMNH); *Madre de Dios*: 15 km E. of Puerto Moldonado on Rio Madre de Dios, 12°17′S, 70°52′W, 4 June 1983, G.C. Hunter, 1 ♀ (CAS); same location & collector, 27 June 1983, 1 ♀ (CAS).

Diagnosis.—This species is distinguished

Table 1.—Eye measurements for species of *Hesydrus* in mm. Measurements are dimensions within outer margins of entities included. AE row = width of anterior eye row, PE row = width of posterior eye row, OQA = width of ocular quadrangle anteriorly (width of anterior median eyes), OQP = width of ocular quadrangle posteriorly (width of posterior median eyes), OQH = height of ocular quadrangle (height of anterior median eye and posterior median eye), PLE = diameter of posterior lateral eye, PME = diameter of posterior median eye, ALE = diameter of anterior lateral eye, AME = diameter of anterior median eye, PLE-PME = interdistance between posterior lateral eye and posterior median eye, PME-PME = interdistance between posterior median eyes, ALE-AME = interdistance between anterior lateral eye and anterior median eye, AME-AME = interdistance between anterior median eyes.

	Hesydrus palustris ♂	*Hesydrus palustris* ♀	*Hesydrus habilis* ♂	*Hesydrus habilis* ♀	*Hesydrus canar* ♂	*Hesydrus canar* ♀	*Hesydrus caripito* ♀	*Hesydrus yacuiba* ♀	*Hesydrus chanchamayo* ♀
AE row	1.12	1.32	1.17	1.20	1.29	1.28	1.18	1.17	1.47
PE row	2.13	2.55	2.20	2.36	2.53	2.50	2.38	2.37	2.94
OQA	0.73	0.81	0.73	0.73	0.83	0.81	0.74	0.72	0.90
OQP	1.20	1.35	1.08	1.13	1.26	1.21	1.20	1.23	1.44
OQH	0.90	0.95	0.90	0.96	1.03	1.04	0.95	0.85	1.10
PLE	0.46	0.49	0.52	0.50	0.54	0.52	0.50	0.45	0.60
PME	0.44	0.44	0.44	0.45	0.47	0.48	0.45	0.41	0.54
ALE	0.18	0.20	0.17	0.20	0.18	0.21	0.20	0.17	0.21
AME	0.31	0.33	0.33	0.45	0.35	0.38	0.32	0.30	0.33
PLE-PME	0.40	0.55	0.37	0.47	0.50	0.51	0.44	0.45	0.55
PME-PME	0.46	0.49	0.35	0.35	0.41	0.37	0.40	0.48	0.48
ALE-AME	0.02	0.05	0.06	0.06	0.07	0.06	0.05	0.06	0.10
AME-AME	0.08	0.20	0.15	0.15	0.19	0.20	0.16	0.19	0.23

by characteristics of the prominent retrolateral tibial apophysis which is about as wide as long and diverges distinctly from the axis of the tibia; its apex is rounded on one corner and acute on the other. Additionally, the guide of the median apophysis is acute and directed distad. The distinctive scape of the epigynum emerges dorsally from beneath a distinct rim, is widest at about the middle of its length, and is rugose on the posterior half. Internally, about one-third of the spermathecum is free from attachment to other structures.

Description.—*Male (lectotype):* Carapace (Fig. 1) medium brown with irregular submarginal light bands, narrow dark marginal bands, black in eye region, length 5.0, width 4.5. Sternum light, unmarked, length 2.30, width 2.15; labium generally light, lighter at distal margin, length 0.45, width 0.42. Clypeus height 0.35, width 2.18. Anterior eye row straight or slightly recurved, eye measurements in Table 1. Cheliceral faces light and shaped as for genus, three retromarginal teeth, subequal in size and with a gap between proximal two. Legs II-IV-I-III, measurements in Table 2. Color of legs medium brown, marked only with very faint maculae on dorsum of femora. Abdomen with distinct, diffuse dorsal pattern (Fig. 1), length 4.7. Palpus (Figs. 2, 3) tibia length approximately equal to length of cymbium, bulb t and st prominent, vd of ma acute distally, g of dd acute, curved distally towards apex of c, ecd of rta prominent, projected somewhat laterally, rounded on outer edge except at ventral corner.

Table 2.—Leg measurements of *Hesydrus palustris* male in mm.

Leg segment	I	II	III	IV
Femur	5.8	7.3	5.8	6.7
Tibia-patella	7.7	9.4	6.9	8.3
Metatarsus	6.2	7.5	5.5	8.5
Tarsus	3.5	4.0	3.6	4.5
Total	23.2	28.2	21.8	28.0

Female (paralectotype): Carapace with irregular light submarginal bands, length 5.6, width 5.5. Sternum unmarked, length 3.1, width 2.8; labium length 1.0, width 0.95. Clypeus unmarked, height 0.50, width 2.5. Anterior eye row slightly recurved, eye measurements in Table 1. Chelicerae medium

Table 3.—Leg measurements of *Hesydrus palustris* female in mm.

Leg segment	I	II	III	IV
Femur	6.9	8.1	7.0	8.0
Tibia-patella	9.0	10.3	8.4	9.9
Metatarsus	6.6	7.4	6.4	9.5
Tarsus	3.6	3.3	4.0	4.5
Total	26.1	29.1	25.8	31.9

brown, three promarginal teeth, three retromarginal teeth with gap between proximal two. Legs unmarked, IV-II-I-III, measurements in Table 3. Abdomen with distinct, diffuse dorsal pattern similar to male, venter light, unmarked, length 7.0. Median scape of epigynum (Figs. 4, 5) emerges from under a rim, widest in middle of its length, rugose at the posterior half, spermatheca free from attachment for one-third of their length.

Variation.—Carapace length of males average 4.74 (4.0–5.3, n = 11) and of females 4.91(3.9–6.2, n = 50). Dorsal pattern similar in both sexes with little variation noted.

Natural history.—Average diameter of 22 egg sacs equals 8.54 (6.1–10.5). Occurrence of egg sacs in the months of February, March, June, September and October suggests that reproduction may occur year round.

Distribution.—Known from the high elevation tributaries of the Amazon River on the Eastern slopes of the Andes in Peru, Equador and Bolivia. A single male specimen from the Canal Zone seems disjunct from the of the main population. A thorough collecting effort at this location at Barro Colorado Island by the author in 1983 failed to find any specimens of *Hesydrus* although other trechaleids were found there suggesting that the Chickering specimen location may be in error. A single female in northern Argentina seems also be disjunct, but further collections are needed to determine if it is part of a continuous distribution (Fig. 6).

Hesydrus habilis (O. P.-Cambridge 1896)
Figs. 7–11

Triclaria habilis O.P.-Cambridge 1896:173, plate 22, fig. 9.

Trechalea habilis (O.P.-Cambridge): F.O.P.-Cambridge 1902:313, plate 30, fig. 15.

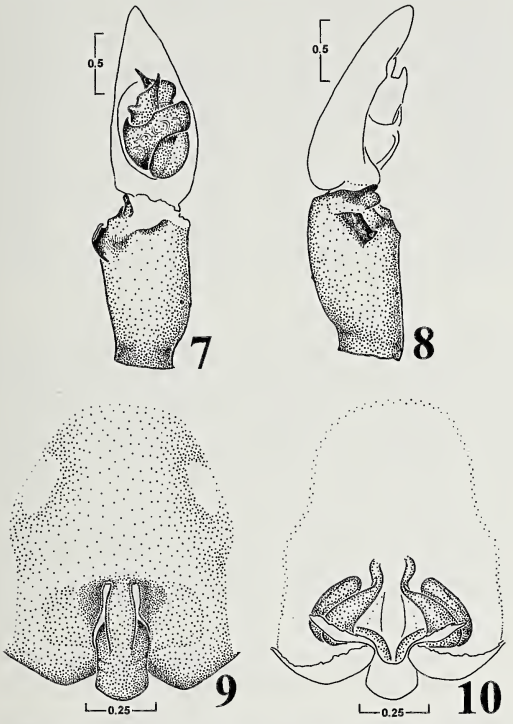
Hesydrus habilis (O.P.-Cambridge): F.O.P.-Cambridge 1903:165, plate 15, fig. 21; Roewer 1954: 137; Bonnet 1957:2182; Platnick 2004.

Type material.—Holotype male, Costa Rica, 1907, by Sarg (BMNH, examined).

Other material examined.—COSTA RICA: unnamed river near Siquirres, 10°06′N, 83°31′W, 16 August 1983, J. Carico & F. Coyle, 7 ♂, 9 ♀ (JEC); Rio Chirripo de Alantica near Limon, 9°46′N, 83°10′W, 16 August 1983, J. Carico & F. Coyle, 4 ♂, 6 ♀ (JEC); 7 miles W. Turrialba, 9°54′N, 83°41′W, 7 August 1927, W.J. Hamilton, Jr., 1 ♂, 4 ♀, 4 juveniles (AMNH); Rio Corobici, 1 km de Carretera Interamer., 10°26′N, 85°10′W, December 1965, C.E. Valerio, 2 ♂, 1 ♀ (UCR). HONDURAS: Lancetilla, 14°54′N, 89°07′W, 19 July 1929, A.M. Chickering, 1 ♀ (MCZ); July 1929, A.M. Chickering, 1 ♂ (MCZ), 11 July 1929, A.M. Chickering, 1 ♀ (MCZ), Lancetilla, Mt. Side near reservoir, 25 July 1929, A.M. Chickering, 1 ♀ (MCZ). PANAMA: Rio Changuinol near Quebrada el Guabo, 8°46′N, 79°56′W, April 1980, C.W. Myers, 1 ♀ (AMNH); Remedios, 8°14′N, 81°51′W, 27 February 1924, A. & W. Petrunkevitch, 1 ♂ (YPM), river 10 km W. David, 8°26′N, 82°26′W, 8 August 1983, J. Carico, F. Coyle, J. Coddington, W. Eberhard, 1 ♂ (JEC).

Diagnosis.—The distinctive small retrolateral tibial apophysis in the male palpus is wider than long, truncated distally, and follows the contour of the tibia. The guide of the median apophysis is directed slightly laterally. The distinctive scape of the female epigynum is continuous with the epigynal plate, not separated by a ridge, and is narrowed in its anterior half.

Description.—*Male (Siquirres, near Rio Pacuare, Costa Rica):* Carapace medium brown with irregular submarginal light bands, narrow dark marginal bands, black in eye region, length 4.8, width 4.8. Sternum light, unmarked, length 2.9, width 2.5; labium generally light, lighter at distal margin, length 0.92, width 0.85. Clypeus height 0.34, width 1.50. Anterior eye row slightly recurved, eye measurements in Table 1. Cheliceral faces light and shaped as for genus, three retromarginal teeth, subequal in size and with a gap between proximal two. Legs II-IV-I-III measurements in Table 4. Color of legs medium brown, marked only with very faint maculae on dorsum of femora. Abdomen with distinct, diffuse dorsal pattern but three pairs of light spots evident, length 4.6. Palpus (Figs. 7, 8) tibia length approximately equal length of



Figures 7–10.—Genitalia of *Hesydrus habilis*. 7, 8. right palpus; 7. ventral view, 8. retrolateral view; 9, 10. female genitalia; 9. ventral view, 10. dorsal view.

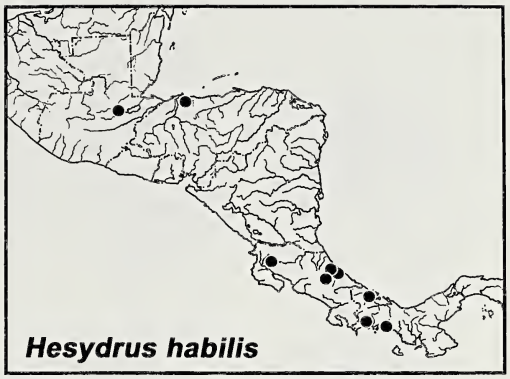


Figure 11.—Distribution of *Hesydrus habilis* in Central America.

cymbium, bulb t and st prominent, vd of ma acute distally, g of dd acute, directed anteriolaterally, ecd of rta prominent, cupped, wider than long, truncated distally following the contour of the tibia, smooth on outer edge.

Female (Siquirres, near Rio Pacuare, Costa Rica): Carapace with irregular light submarginal bands, narrow dark marginal bands, length 5.0, width 5.0. Sternum unmarked, length 2.9, width 2.7; labium length 1.00, width 0.92, lighter distally. Clypeus unmarked, height 0.39, width 2.45. Anterior eye row slightly recurved, eye measurements in Table 1. Chelicerae medium brown, unmarked, three promarginal teeth, three retromarginal teeth equidistant, equal size. Legs IV-II-I-III, measurements in Table 5. Abdomen with distinct, diffuse dorsal pattern similar to male, venter light, unmarked, length 5.1. Median scape of epigynum (Figs. 9, 10) narrow, continuous with the epignal plate, not separated by a ridge, narrower in the anterior half, internal structures as for genus. The scape is continuous with the epigynal plate, not separated by a ridge, and narrowed in its anterior half.

Variation.—Carapace length of males average 4.79 (4.2–5.2, n = 14) and of females 4.68 (4.0–5.4, n = 23). Dorsal pattern similar in both sexes with little variation noted.

Natural history.—Twelve egg sacs collected during the months of April, July, August, and December have an average diameter of 8.37 (7.1–10.2).

Distribution.—Central Guatemala, Costa Rica and western Panama (Fig. 11).

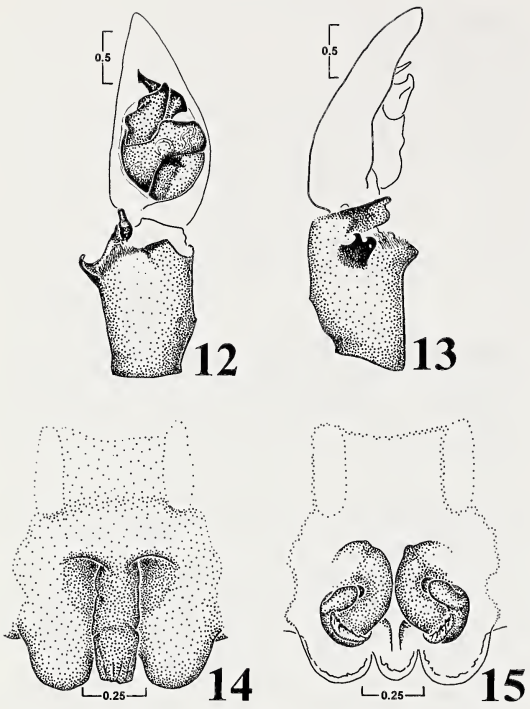
Hesydrus canar new species
Figs. 6, 12–15

Type material.—Holotype male, Rio Yanayacu, Cañar, Ecuador, 2°27′S, 79°17′W, 22 September 1984, F. Man Ging (MECN). Paratypes: 3 males, 2 females, same collection data as holotype (MECN).

Other material examined.—COLOMBIA: *Cauca*: Questrada Huanqui, Rio Saija area, 2°56′N, 77°38′W, 18 October–3 November 1971, 4 ♀ (FMNH). ECUADOR: *Guyas*: Hac, San Juaquin, 4 km SW. Bucay, 2°41′S, 79°40′W, 1–4 May 1986, S.H. Kamey, 3 ♀ (MECN); *El Oro*: Rio Colorado, 0°41′N,

Table 4.—Leg measurements of *Hesydrus habilis* male in mm.

Leg segment	I	II	III	IV
Femur	6.2	7.7	6.2	7.0
Tibia-patella	8.3	10.1	7.4	9.0
Metatarsus	6.4	8.0	6.0	9.0
Tarsus	3.0	3.7	3.3	4.4
Total	23.9	29.5	22.9	29.4



Figures 12–15.—Genitalia of *Hesydrus canar*. 12, 13. right palpus; 12. ventral view, 13. retrolateral view; 14, 15. female genitalia; 14. ventral view, 15. dorsal view.

77°58′W, 3 November 1942, R. Walls, 1 ♀ (CAS); *Pichincha*: Macachi, 0°10′S, 78°40′W, March 1943, H. Frizzell, 1 ♀ (CAS). PERU: *Piura*: Higueron Las Lomas, 4°39′S, 80°14′W, 29 July 1941, H. & F. Frizzell, 2 ♂, 2 ♀ (CAS); Quiroz River, 4°26′S, 80°18′W, 26 December 1940, H. & F. Frizzell, 1 ♀ (CAS).

Etymology.—The name is a noun in apposition suggested by the name of the province from which the specimen was collected.

Diagnosis.—The distinctive retrolateral apophysis of the male palpus is about as long as wide and distinctly bifurcated distally. Also, the guide of the median apophysis has a distinctive spur near the tip. The scape of the epigynum is rather uniform in width and is continuous with the epigynal plate while not separated from it by a rim, slightly narrowed medially.

Description.—*Male (holotype):* Carapace medium brown with distinct zig-zag submarginal light bands, dark marginal bands with undulations into the submarginal band, black in eye region, length 5.7, width 5.4. Sternum light, unmarked, length 3.1, width 2.8; labium median brown, lighter at distal margin, length 1.15, width 0.93. Clypeus height 0.40, width 2.75. Anterior eye row slightly recurved, eye measurements in Table 1. Cheliceral faces light and shaped as for genus, three retromarginal teeth, subequal in size and with a gap between proximal two. Legs II-IV-I-III, measurements in Table 6. Color of legs medium brown, marked only with distinct maculae on dorsum of femora. Abdomen mostly dark above with distinct, diffuse light areas in pattern, length 5.1. Palpus (Figs. 12, 13) tibia length approximately equal length of cymbium, bulb t and st prominent, vd of ma acute distally, g of dd with ante-apical spur, directed anterio-laterally, ecd of rta prominent, bifurcated with each division acute and curved dorsally.

Table 5.—Leg measurements of *Hesydrus habilis* female in mm.

Leg segment	I	II	III	IV
Femur	6.5	8.0	6.4	7.3
Tibia-patella	8.4	10.3	7.7	9.2
Metatarsus	6.3	8.0	6.4	9.2
Tarsus	3.2	3.8	3.6	4.9
Total	24.4	30.1	24.1	30.6

Female (paratype): Carapace medium brown with narrow, distinct zig-zag submarginal light bands, dark marginal bands with undulations into the submarginal band, black in eye region, length 5.4, width 5.4. Sternum light, unmarked, length 3.1, width 2.8; labium length 1.08, width 1.00, lighter distally. Clypeus unmarked, height 0.41, width 2.60. Anterior eye row slightly recurved, eye measurements in Table 1. Chelicerae dark brown, unmarked, three promarginal teeth, on the left side three retromarginal teeth, subequal in size and with a gap between proximal two, two submarginal teeth on the right side. Legs IV-II-I-III, measurements in Table 7. Color of legs medium brown, marked only with distinct maculae on dorsum of femora. Abdomen dorsal pattern similar to male, venter light, unmarked, length 8.1. Median scape of epigynum (Figs. 14, 15) rather uniformly narrow, continuous with the epigynal plate and not separated by a rim, internal structures as for genus.

Variation.—Carapace length of males average 5.54 (5.0–6.0, n = 5) and of females

Table 6.—Leg measurements of *Hesydrus canar* male in mm.

Leg segment	I	II	III	IV
Femur	7.0	8.6	6.9	8.0
Tibia-patella	9.5	11.5	8.4	10.0
Metatarsus	7.5	9.5	7.0	10.5
Tarsus	3.8	4.5	4.0	5.4
Total	27.8	34.1	26.3	33.9

5.08 (4.2–5.5, n = 13). Dorsal pattern similar in both sexes with little variation noted.

Natural history.—Average diameter of 4 egg sacs equals 7.9 (6.9–8.5). Egg sacs occurred in the months of May, September and October.

Distribution.—Known from the high altitude tributaries of coastal rivers on the Western slopes of the Andes in Columbia, Ecuador and Peru (Fig. 6).

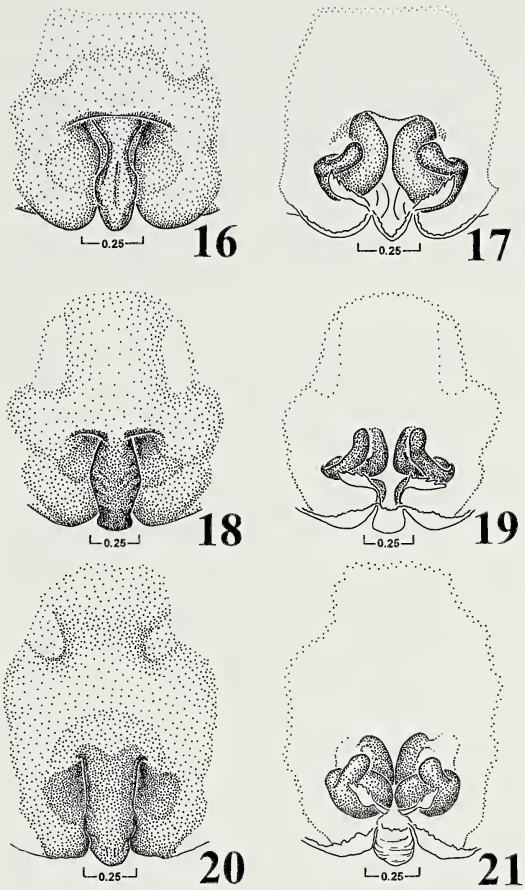
Hesydrus caripito new species
Figs. 6, 16–17

Type.—Holotype female, Caripito, Monagas, Venezuela, 10°07′N, 63°06′W, 17 March 1942, New York Zoological Society 1942 Venezuela Expedition (AMNH).

Etymology.—The name is a noun in apposition suggested by the name of the type locality.

Diagnosis.—Distinctive characters of the median scape of the female epigynum include being very narrowed near the base, emerging from beneath the transverse rim, and its length being greater than half the length of the entire sclerotized epigynal plate.

Description.—*Female (holotype):* Carapace medium brown with indistinct submarginal light bands, indistinct medium submarginal band, black in eye region, length 4.9, width 5.0. Sternum light, unmarked, length 2.9, width 2.6; labium lighter distally, length 1.00, width 0.90. Clypeus unmarked, height 0.36, width 2.40. Anterior eye row slightly recurved, eye measurements in Table 1. Chelicerae dark brown, unmarked, three promarginal teeth, three equidistant retromarginal teeth, subequal in size. Legs IV-II-I-III, measurements in Table 8. Color of legs medium brown, marked only with distinct maculae on dorsum of femora. Abdomen dorsal pattern diffuse and distinct, venter light, unmarked, length 5.5. Median scape of epigynum (Figs. 16, 17) narrowed basally, epigynal plate relatively short, internal structures as for genus.



Figures 16–21.—Female genitalia of *Hesydrus* species. 16, 17. *H. caripito*; 16. ventral view, 17. dorsal view; 18, 19. *H. yacuiba*; 18. ventral view, 19. dorsal view; 20, 21. *H. chanchamayo*; 20. ventral view, 21. dorsal view.

Natural history.—A note with the collection states: "Under and around smooth stones in ford across Caripe R. at water pump station."

Material examined and distribution.—Known only from the type specimen from Venezuela (Fig. 6).

Hesydrus yacuiba new species
Figs. 6, 18, 19

Type material.—Holotype female, Yacuiba, Tarija, Bolivia, 22°02′S, 63°41′W, 18 November 1961, Bachmann (MACN).

Etymology.—The name is a noun in apposition suggested by the name of the type locality.

Table 7.—Leg measurements of *Hesydrus canar* female in mm.

Leg segment	I	II	III	IV
Femur	6.8	8.3	6.8	7.8
Tibia-patella	8.9	10.7	8.0	9.5
Metatarsus	6.8	8.4	6.5	9.3
Tarsus	3.6	4.1	3.9	5.1
Total	26.1	32.5	25.2	31.7

Table 8.—Leg measurements of *Hesydrus caripito* female in mm.

Leg segment	I	II	III	IV
Femur	5.8	7.2	6.0	6.8
Tibia-patella	7.8	9.3	7.2	8.3
Metatarsus	5.9	7.5	5.7	8.5
Tarsus	2.8	3.5	3.3	4.2
Total	22.3	27.5	22.2	27.8

Diagnosis.—The scape of the female epigynum is continuous with the epigynal plate, widest midway along its length and expanded slightly at the posterior end. The entire ventral surface is rugose.

Description.—*Female (holotype):* Carapace medium brown with indistinct submarginal light bands, white hairs on clypeus, eye region and submarginal band, black in eye region, length 4.7, width 5.1. Sternum light, unmarked, length 2.8, width 2.8; labium, lighter distally, length 1.00, width 0.90. Clypeus unmarked but with white hairs, height 0.44, width 2.42. Anterior eye row slightly recurved, eye measurements in Table 1. Chelicerae medium, unmarked, covered in dense light and dark hairs, three promarginal teeth, three equidistant retromarginal teeth, subequal in size. Legs II-IV-I-III, measurements in Table 9. Color of legs medium brown, marked only with distinct maculae on dorsum of femora. Abdomen dorsal pattern diffuse and distinct, covered in dense shiny hairs, venter light, unmarked, length 5.1. Median scape of epigynum (Figs. 18, 19) rough-surfaced, narrowed proximally and distally, internal structures as for genus.

Natural history.—Unknown.

Material examined and distribution.—Known only from the type specimen from Bolivia (Fig. 6).

Hesydrus chanchamayo new species
Figs. 6, 20, 21

Type material.—Holotype female, Chanchamayo, Ica, Peru, 13°42′S, 75°48′W, 7 February 1953, Weyrauch (CAS).

Etymology.—The name is a noun in apposition suggested by the name of the type locality.

Diagnosis.—The rather smooth median scape of the female epigynum has its continuous connection with the epigynal plate broader than the width of the scape and not separated by a rim. The internal structures, including the short spermathecum, are heavily sclerotized and robust. This specimen is larger (carapace length 6.5) than any other female in the genus thus far studied.

Description.—*Female (Holotype):* Carapace medium brown with indistinct submarginal light bands, indistinct medium band, black in eye region, length 6.5, width 6.7. Sternum light, unmarked, length 1.90, width 1.70; labium length 1.24, width 1.70, lighter distally. Clypeus unmarked, height 0.60, width 3.0. Anterior eye row slightly recurved, eye measurements in Table 1. Chelicerae dark brown, unmarked, three promarginal teeth, three equidistant retromarginal teeth, subequal in size. Legs II-III-I (IV missing), measurements in Table 10. Color of legs medium brown, marked only with indistinct maculae on dorsum of femora. Abdomen dorsal pattern diffuse and distinct, venter light, unmarked, length 9.2. Median scape of epigynum (Figs. 20, 21) of relatively uniform width and not separated from epigynal plane by a sclerotic rim, internal structures as for genus but heavily sclerotized and robust.

Natural history.—Unknown.

Material examined and distribution.—Known only from the type specimen from Peru. There are at least three localities by the same name in the highlands of Eastern Peru

Table 9.—Leg measurements of *Hesydrus yacuiba* female in mm.

Leg segment	I	II	III	IV
Femur	6.0	7.6	6.2	6.9
Tibia-patella	7.9	9.5	7.3	8.5
Metatarsus	5.6	7.3	5.8	8.2
Tarsus	3.3	3.7	3.4	4.0
Total	22.8	28.1	22.7	27.6

Table 10.—Leg measurements of *Hesydrus chanchamayo* female in mm. Leg IV missing.

Leg segment	I	II	III	IV
Femur	7.9	9.7	8.2	—
Tibia-patella	10.5	12.4	9.7	—
Metatarsus	7.6	9.6	7.7	—
Tarsus	4.3	5.3	4.9	—
Total	30.0	37.0	30.5	—

and east of the Andean continental divide (Fig. 6). Location on the map is arbitrarily central to these localities and intended only to show a general geographic reference to the other species.

ACKNOWLEDGMENTS

Thanks are extended to the following persons and museums for the loan of specimens: A. Kury (MNRJ), C.F. Ituarte (MLP), N.I. Platnick (AMNH), H.W. Levi (MCZ, and via MECN), the late M.E. Galiano (MACN), C. Griswold and D. Ubick (CAS), C. Rollard (MNHN), P. Sierwald (FMNH), L.W. Buss (YPM) and C.E. Valerio (UCR). I thank also R. Balm (Rutgers Univ.) who provided valuable information on the itinerary of the Yale 1911 Peruvian Expedition, and to the editors, two anonymous reviewers, N.A. Carico and E.L. Cruz da Silva for corrections and suggested improvements.

LITERATURE CITED

Bonnet, P. 1957. Bibliographia Araneorum. Toulouse 2(3):1927–3026.

Bonnet, P. 1959. Bibliographia Araneorum. Toulouse 2(5):4231–5058.

Brignoli, P.M. 1983. A Catalogue of the Araneae Described Between 1940 and 1981. (P. Merrett, ed.).Manchester University Press, Manchester.

Cambridge, F.O.P.- 1902. Arachnida—Araneida and Opiliones. Pp. 313–424. *In* Biologia Centrali-Americana, Zoology, vol. 2 (F.D. Godman & O. Salvin, eds.). Taylor and Francis, London.

Cambridge, F.O.P.- 1903. On some new species of spiders belonging to the families Pisauridae and Senoculidae; with characters of a new genus. Proceedings of the Zoological Society of. London 1903:151–168.

Cambridge, O.P.- 1896. Arachnida. Araneida. Pp. 161–224. *In* Biologia Centrali-Americana, Zoology, vol. 1 (F.D. Godman & O. Salvin, eds.). Taylor and Francis, London.

Cambridge, O.P.-. 1897. Arachnida. Araneida. Pp. 225–232. *In* Biologia Centrali-Americana, Zoology, vol. 1 (F.D. Godman & O. Salvin, eds.). Taylor and Francis, London.

Caporiacco, L. di 1947. Diagnosi preliminari di specie nuove de arachnidi della Guiana Britannica. Monitore Zoologico Italiano 56:20–24.

Carico, J.E. 1986. Trechaleidae: A "new" American spider family. Pp. 305. *In* Proceedings of the Ninth International Congress of Arachnology, Panama 1983. (W.G. Eberhard, Y.D. Lubin & B.C. Robinson, eds.). Smithsonian Institution Press, Washington, D.C.

Carico, J.E. 1993. Revision of the genus *Trechalea* Thorell (Araneae, Trechaleidae) with a review of the taxonomy of the Trechaleidae and Pisauridae of the Western Hemisphere. Journal of Arachnology 21:226–257.

Carico, J.E. 2005. Descriptions of two new spider genera of Trechaleidae (Araneae, Lycosoidea) from South America. Journal of Arachnology 33: 795–810.

Chamberlin, R.V. 1916. Results of the Yale Peruvian Expedition of 1911. The Arachnida. Bulletin of the Museum of Comparative Zoology at Harvard College, Cambridge 60(6):177–299.

Koch, C.L. 1848. Die Arachniden. Füntzehnter Band. Nürnberg 210 pp.

Lehtinen, P.T. 1967. Classification of the cribellate spiders and some allied families, with notes on the evolution of the suborder Araneomorpha. Annales Zoologici Fennici 4:199–468.

Mello-Leitão, C.F. 1931. Arachnidos do Rio Grande do Sul. Boletin Biologico Rio de Janeiro, São Paulo 17:10–14.

Mello-Leitão, C.F. 1941. Las arañas de Córdoba, La Rioja, Calamarca, Tucumán, Salta y Jujuy colectadas por los Profesores Birabén. Revista del Museo de La Plata 2:99–198.

Platnick, N. I. 2004. The World Spider Catalog, Version 4.5. American Museum of Natural History, online at http://research.amnh.org/entomology/spiders/catalog/index.html

Roewer, C.F. 1954. Katalog der Araneae, vol. 2a. Institut Royal des Sciences Naturelles de Belgique, Bruxelles.

Pocock, R.I. 1900. Myriapoda and Arachnida. In Report on a collection made by MM. F.V. McConnell and J.J. Quelch at Mount Roriama in British Guiana. Transaction of the Linnean Society of London. Zoology 2:64–71.

Sierwald, P. 1989. Morphology and ontogeny of female copulatory organs in American Pisauridae with special reference to homologous features (Arachnida: Araneae). Smithsonian Contributions to Zoology 484:1–24.

Sierwald, P. 1990. Morphology and homologous features in the male palpal organ in Pisauridae and other spider families with notes on the taxonomy of Pisauridae (Arachnida: Araneae).

Nemouria, Occasional Papers of the Delaware Museum of Natural History 35:1–59.

Sierwald, P. 1993. Revision of the spider genus *Paradossenus*, with notes on the family Trechaleidae and the subfamily Rhoicininae (Araneae: Lycosoidea). Revue Arachnologique 10(3):53–74.

Simon, E. 1898a. Descriptions d'arachnides nouveaux des familles des Agelenidae, Pisauridae, Lycosidae et Oxyopidae. Annales de la Société Entomologique de Belgique, Bruxelles 42:1–34.

Simon, E. 1898b. Histoire Naturelle des Araignées. Vol. 2(2), pp. 193–380, Encyclopédie Roret, Paris.

Simon, E. 1903. Histoire Naturelle des Araignées. Vol. 2(4), pp. 699–1080, Encyclopédie Roret, Paris.

Manuscript received 8 December 2003, revised 26 August 2004.

2005. The Journal of Arachnology 33:797–812

DESCRIPTIONS OF TWO NEW SPIDER GENERA OF TRECHALEIDAE (ARANEAE, LYCOSOIDEA) FROM SOUTH AMERICA

James E. Carico: School of Science, Lynchburg College, 1501 Lakeside Drive, Lynchburg, Virginia 24501 USA. E-mail: carico@lynchburg.edu

ABSTRACT. Two new genera in the spider family Trechaleidae, *Trechaleoides* and *Paratrechalea*, are described. The females of the two known species of *Trechaleoides*, *T. keyserlingi* (F.O.P.-Cambridge) (type species) and *T. biocellata* (Mello-Leitão) are redescribed and their respective males are described for the first time; both are transferred from *Trechalea*. Two additional previously described species, also both transferred from *Trechalea*, are herein placed in the genus *Paratrechalea* are redescribed from their types, i.e., the female of *P. ornata* (Mello-Leitão) (type species) and male of *P. wygodzinskyi* (Soares & Camargo). The male of *P. ornata* is described for the first time. Four new species of *Paratrechalea*, *P. longigaster*, *P. galianoae*, and *P. azul* from females, and *P. saopaulo* from males and females are described. The immature specimen historically regarded as the holotype of *Trechalea longitarsis* (C.L. Koch) and regarded as a mistaken identity, is an unidentified species of *Trechaleoides*. The female holotype of *Trechalea limai* Mello-Leitão is confirmed to be lost but is considered to be a member of the genus *Paratrechalea* based on a study of the original description.

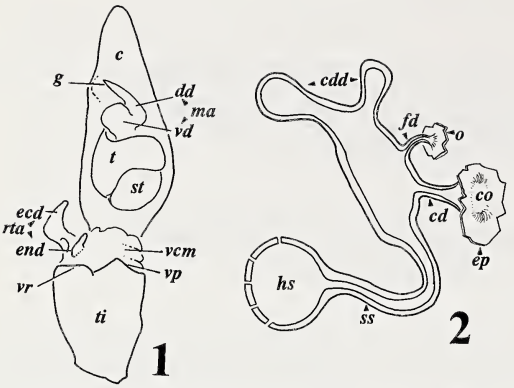
Keywords: Trechaleidae, *Trechaleoides*, *Paratrechalea*, new genera, new species

Since the reintroduction of Simon's (1890) family Trechaleidae (Carico 1986), its validity has been confirmed through the work of others (Sierwald 1990 [Trechaleidae not recognized but acknowledged as a distinct "*Trechalea* genus-group"], 1993, 1997; Coddington & Levi 1991 [cladistic analysis]; Griswold 1993 [cladistic analysis]). Beginning with the redefinition of the family along with a revision of its type genus *Trechalea* Thorell 1869 (Carico 1993), the goal was to reveal the taxonomy of the remaining members of this unique family through revisions of the included genera. The current work represents an additional step towards this goal.

In this work, two new genera are erected to include species (specified below) that were previously placed into *Trechalea* and additionally to contain species not previously described. In the process of defining these genera, references are made to characters used in the previously mentioned study of the genus *Trechalea* in order to further develop and refine a set of characters that will ultimately distinguish among all the closely-related monophyletic genera of the family (*sensu* Carico 1993).

These two new genera share with *Trechalea*, and no other genus identified in the family, the characteristic of having only the tarsi flexible. However, the characteristics of the genitalia clearly distinguish these new genera from each other as well as from *Trechalea*. To distinguish the males from those of *Trechalea*, the median apophysis of the palpal bulb (Fig. 1) has a less complex ventral division in the former species. Additional features of this structure, detailed below, will distinguish between the new genera. In females of these new genera, a typical middle field of the female epigynum (Figs. 6, 20), present in *Trechalea* is absent; instead, there is a pronounced scape. Internally the notable differences with *Trechalea* are that the spermathecae are free and that pairs of diverticula (rather than only one) arise from a common chamber. Additional details of the external and internal structures of the female genitalia, as reported below, will distinguish between the new genera.

Little is known about the biology of representatives of these genera. However, there are indications from fragmentary evidence that these genera share a feature with *Trechalea*, i.e., they apparently occupy a semi-aquatic habitat based on references to place names of streams on the collection labels. The



Figures 1, 2.—Diagrammatic genitalia of *Trechaleoides* and *Paratrechalea*. 1. right palpus, ventral view; 2. internal structures of female genitalia. (Abbreviations explained in text)

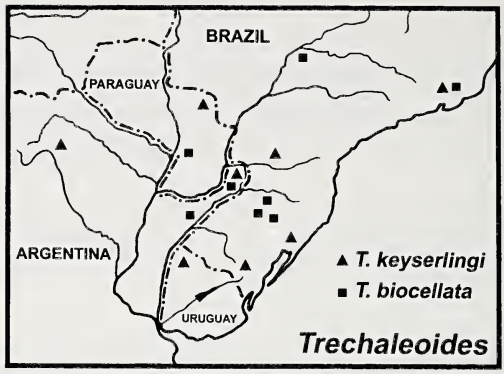


Figure 3.—Distribution of species of *Trechaleoides*.

unique structure of the egg sac and manner of carrying the spiderlings on it while attached to the spinnerets, first described for *Trechalea extensa* (O.P.-Cambridge) by Berkum (1982), is apparently also confirmed as a characteristic of the family. This conclusion derives from an assumption that the details of the egg sac's structure, as described by Carico (1993) for *Trechalea* and presumed to be a family trait, is consistent with the structure of egg sacs found with specimens of the new genera.

The distributions of these two genera overlap in a region of South America between 15°S and 35°S latitude, an area which includes regions of southern Brazil, northern Argentina, and Paraguay and is locally known as the "Cone Sul" (Southern Cone). Therefore, it appears that their distribution is primarily related to streams of the lower Rio la Plata river basin and the several smaller coastal streams. From a preliminary overview of the distributions of all trechaleid genera in South America, the two new genera considered herein may be the predominant representatives of the family in this region. Two species of Mello-Leitão from this region, *Trechalea limai* Mello-Leitão 1941 and *T. syntrechaleoides* Mello-Leitão 1941, whose types were previously unobtainable from the Museu Nacional, Rio de Janeiro during a previous study (Carico 1993) were never the less regarded to be misplaced in *Trechalea*. Recently, access to these specimens was obtained resulting in a conclusion that *T. limai* is lost and probably destroyed (A.B. Kury pers. comm.). Careful analysis of the description of *T. limai* reveals that it is a species *nomen dubium* in the genus *Paratrechalea*. *Trechalea syntrechaleoides*, however, is not congeneric with the genera in this report, and its status will be treated elsewhere in a separate generic revision.

The nomenclature of the genitalia and other anatomical features follow Carico (1993 [genitalic terminology after Sierwald 1989, 1990]). Because of its rigidity and relative resistance to distortion, carapace length is emphasized as an index of body size, particularly in discussions of variation. Measurements and scales are in millimeters.

Specimens examined during this study are lodged in the following museums: Museu de Zoologica da Universidad de São Paulo (MZUSP); Museum of Comparative Zoology, Harvard (MCZ); Natural History Museum, London (BMNH); Museu de Ciências Naturais, Porto Alegre (MCN); Museo Argentina de Ciencias Naturales, Buenos Aires (MACN); Museo Nacional de Historia Natural, Montevideo (MNHN); Museo de la Universidad Nacional de la Plata (MLP); Museu Nacional, Rio de Janeiro (MNRJ); Universidade Federal do Rio Grande do Sul, Porto Alegre (UFRGS), and Peabody Museum of Natural History, New Haven (PMNH).

Trechaleoides new genus

Type species.—*Trechalea keyserlingi* F.O.P.-Cambridge 1903.

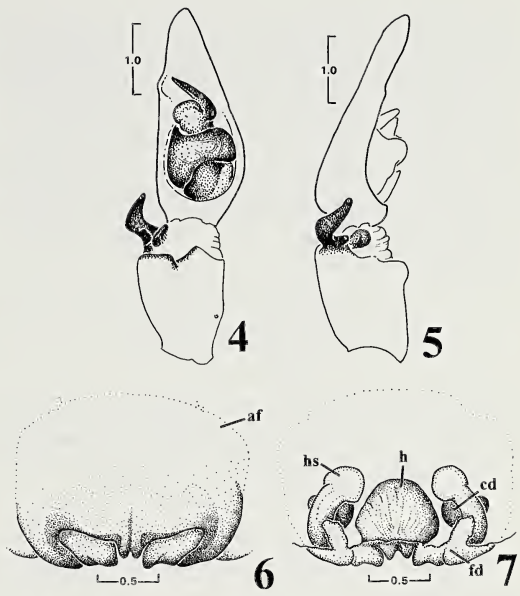
Etymology.—The feminine generic name indicates its relationship with the genus *Trechalea*.

Diagnosis.—*Trechaleoides* can be distinguished from all other described genera of

Trechaleidae (*sensu* Carico 1993) by a combination of characters. In the male palpus, the ventral division (vd) of the median apophysis (ma) is a simple, small, rounded projection rather than angular, and the guide (g) is conspicuous, more slender and tapered than in *Trechalea* and *Hesydrus*. The ventral division is also simplified and rounded in *Paratrechalea* but it is much expanded there. The epigynum is distinguished by a pair of small posterio-lateral projections separated by sutures from the middle anterior field, and by details of the internal female genitalia including a posterio-median hood-like chamber. A small retromarginal tooth is adjacent to the most proximal tooth and offset into the fang furrow. These are relatively large spiders with the carapace length ranging from 6.1–11.0.

Description.—Carapace moderately low, cephalic area not distinct, AE row straight or slightly recurved. Each basal segment of male chelicera not swollen anteriorly and without a lateral carina; promarginal teeth three with center one largest, five retromarginal teeth (occasionally four) with a smaller tooth offset between the proximal two into the fang furrow. Leg lengths variable but III always shortest while others often subequal, only tarsi flexible, all claws dentate, paired ventral macrosetae on tibia.

Male palpal bulb (Fig. 1) median apophysis (ma) with distal, curved sickle-shaped dorsal division (dd) narrow, tapered, with tip conspicuous, and directed ventrad, a small, rounded ventral division (vd) of variable size but shape distinctive for each species; retrolateral tibial apophysis (rta) arising distally and laterally from near the ventro-distal rim (vr) with ectal division (ecd) divided into two subdivisions, dorsal one longer and curved and ental division (end) partly surrounded by ventral cymbio-tibial membrane (vcm); tibial ventral rim (vr) of ventral protuberance (vp) folded over to create a particularly deep depression in the ventral cymbio-tibial membrane (vcm). The epigynum (Fig. 6) is a slightly convex, nearly circular anterior field (af) with pair of small projections at posterior margin whose long axes tend to transverse, middle field (mf) absent; internally (Figs. 2, 7) the stalked spermathecum head (hs) large and not attached to other components; a pair of diverticula arising from a large common chamber (probably enlarged portion of copulatory duct), both copulatory duct (cd) and fertilization duct (fd) arising from this common chamber; large, hood-shaped structure (h) located posteriomedially.



Figures 4–7.—Genitalia of *Trechaleoides keyserlingi*. 4, 5. right palpus; 4. ventral view, 5. retrolateral view; 6, 7. female genitalia; 6. ventral view, 7. dorsal view. af = anterior field, cd = copulatory duct, fd = fertilization duct, h = hood, hs = head of spermathecum, mf = middle field.

Natural history.—Egg sacs show the basic trechaleid construction as described for *Trechalea* (Carico 1993, fig. 6), i.e., a flattened disc with a peripheral "skirt". The aquatic habitat preference is suggested by the reference to "Arroyo" or "Rio" on some collection labels and is consistent with what is known of other genera, i.e.; *Trechalea* (Carico 1993), *Hesydrus* (pers. obs.), and *Paradossenus* F.O.P.-Cambridge 1903 (Brescovit et al. 2000).

Distribution.—Found in South America southward from the Brazilian state of Minas Gerais into Paraguay, northern Argentina, and Uruguay (Fig. 3).

Remarks.—The specimen mistakenly regarded by F.O.P.-Cambridge (1903) as the type of *Trechalea longitarsis* is actually an immature female of this new genus (Carico 1993) as indicated by the unique characters of retromarginal teeth of the chelicerae, particularly by the presence of a small tooth placed into the fang furrow between the proximal two

larger teeth. Although the typical number of retromarginal teeth is five, there are specimens which have four on one of the chelicera. The locality label with that specimen, "Brazil," is also consistent with the location of this genus. Because of immaturity and the general poor condition of this specimen, it cannot be confidently attributed to any of the species recognized in this work.

Trechaleoides keyserlingi
(F.O.P.-Cambridge 1903)
Figs. 3–7

Trechalea keyserlingi F.O.P.-Cambridge 1903:163, plate 15, figs. 1, 2; Roewer 1954:142; Bonnet 1959:4679; Petrunkevitch 1911:549; Carico 1993:237 (non *Trechalea*); Platnick 2004.

Type material.—Holotype female, Rio Grande do Sul, Brazil, Keyserling (BMNH, examined).

Material examined.—ARGENTINA: *Tucumán*: San Pedro de Colalao, 26°22′S, 65°57′W, March 1967, A. Barrio, 1 ♀ (MACN); *Misiones*: Puali, 27°00′S, 55°00′W, Sciap, J. Carlo?, 1 ♀ (MACN). BRAZIL: *Rio Grande do Sul*: São Jerônimo-Fazenda Casa Branca, 29°58′S, 51°43′W, 20-21 May 1982, J.E. Hennig, 1 ♂ (MCN #10373); São Leopoldo, 29°46′S, 51°09′W, 25 March 1983, C.J. Becker, 1 ♂ (MCN #11517); no locality, 28 October 1981, A.A. Lise, 1 ♀ (MCN #9955); state unknown, 22 November 1987, A.D. Brescovit, 2 ♀ (MCN #17222). PARAGUAY: near Pedro Juan Caballero, 23°00′S, 56°00′W, 25-27 November 1956, C.J.D. Brown, 1 ♀ (MCZ). URUGUAY: *Salto*: Rio Arapey, 30°55′S, 57°49′W, 13 December 1954, collector unknown, 1 ♀ (MNHN).

Diagnosis.—Females of this species are distinguished by the pair of posterior protuberances of the epigynum which are smooth and not folded, and males by the palpal tibia which is approximately half the length of the cymbium.

Description.—*Male (São Jerônimo, Rio Grande do Sul, Brazil):* Carapace medium brown with wide submarginal light bands, dark marginal bands widening posteriorly, black in eye region, length 7.9, width 7.0. Sternum light, with median dusky band on anterior two-thirds, length 4.2, width 3.7; labium reddish-brown, lighter at distal margin, length 1.57, width 1.30. Clypeus height 0.88, width 3.20. Anterior eye row slightly recurved, a cluster of bristles posterior to each PLE, eye measurements in Table 1. Cheliceral faces medium reddish-brown, each with a dark longitudinal band clothed with scattered light and dark hairs, five retromarginal teeth, subequal in size except smaller fifth one between first and third offset into the fang groove. Legs II-IV-I-III, measurements in Table 2, ventral macrosetae pairs on tibiae I-4, II-4, III-3, IV-3. Color of legs medium brown, marked only with faint maculae on dorsum of each femur. Abdomen hairless above (probably rubbed) with distinct dorsal pattern, length 8.0. Palpus (Figs. 4, 5) tibia length approximately half length of cymbium, bulb t and st prominent, vd of ma flattened, moderate-sized, rounded in outline, and not covering the dd, ecd of rta prominent and angular.

Female (holotype): Carapace light with submarginal bands, broad dark median band divided longitudinally by a narrow median band widened between eyes and thoracic grooves, length 9.0, width 8.2. Sternum unmarked, length 5.0, width 4.2; labium length 1.65, width 1.60. Clypeus dark medially and light laterally, height 1.11, width 2.84. Anterior eye row slightly recurved, eye measurements in Table 1. Chelicerae dark and clothed with light hair, three promarginal teeth, five retromarginal teeth on right side and five on left, the smallest ones next to the most proximal teeth. Legs IV-II-I-III, measurements in Table 3, femora with irregular dark maculae, all other segments dark; tarsi flexible, spines not longer than one-third of respective segment. Abdomen dark median band with distinct lateral indentations in the posterior third, sides light with scattered maculae, venter light length 11.0. Pair of smooth projections at posterior margin of epigynum (Figs. 6, 7), internal structures as for genus.

Variation.—Carapace length of males average 7.17 (6.6–7.9, $n = 3$) and of females 7.13 (6.1–8.8, $n = 10$). Dorsal pattern similar in both sexes with little variation noted.

Natural history.—An egg sac from near Pedro Juan Caballero, Paraguay, collected late November, measured 15.0.

Distribution.—Northern Argentina, eastern tributaries of Rio Paraná in southern Paraguay and southern Brazil. Also, in some coastal drainages of southern Brazil (Fig. 3).

Remarks.—According to F.O.P.-Cambridge (1903), the type specimen was originally iden-

Table 1.—Eye measurements for species of *Trechaleoides* and *Paratrechalea* in mm. Measurements are dimensions within outer margins of entities included. AE row = width of anterior eye row, PE row = width of posterior eye row, OQA = width of ocular quadrangle anteriorly (width of anterior median eyes), OQP = width of ocular quadrangle posteriorly (width of posterior median eyes), OQH = height of ocular quadrangle (height of anterior median eye and posterior median eye), PLE = diameter of posterior lateral eye, PME = diameter of posterior median eye, ALE = diameter of anterior lateral eye, AME = diameter of anterior median eye, PLE-PME = interdistance between posterior lateral eye and posterior median eye, PME-PME = interdistance between posterior median eyes, ALE-AME = interdistance between anterior lateral eye and anterior median eye, AME-AME = interdistance between anterior median eyes. ("—" = not observed).

	Trechaleoides keyserlingi ♂	*Trechaleoides keyserlingi* ♀	*Trechaleoides biocellata* ♂	*Trechaleoides biocellata* ♀	*Paratrechalea ornata* ♂	*Paratrechalea ornata* ♀	*Paratrechalea wygodzinskyi* ♂	*Paratrechalea longigaster* ♀	*Paratrechalea galianoae* ♀	*Paratrechalea azul* ♀	*Paratrechalea saopaulo* ♂	*Paratrechalea saopaulo* ♀
AE row	1.40	1.70	1.70	1.50	0.79	0.80	1.14	0.80	0.84	1.11	0.78	0.76
PE row	2.46	3.12	3.1	2.76	1.50	1.45	1.96	1.44	1.64	1.90	1.45	1.46
OQA	0.75	0.90	0.90	0.81	0.44	0.44	0.58	0.40	0.46	0.57	0.40	0.38
OQP	1.15	1.35	1.45	1.33	0.73	0.70	1.03	0.75	0.83	0.96	0.72	0.76
OQH	1.06	1.37	1.28	1.14	0.61	0.58	0.94	0.61	0.70	0.84	0.62	0.60
PLE	0.50	0.60	0.60	0.55	0.32	0.26	0.44	0.25	0.35	0.41	0.33	0.33
PME	0.50	0.59	0.53	0.52	0.30	0.27	0.45	0.25	0.36	0.38	0.35	0.34
ALE	0.27	0.30	0.20	0.25	0.16	0.15	0.21	0.15	0.15	0.21	0.15	0.16
AME	0.33	0.39	0.36	0.37	0.17	0.17	0.26	0.17	0.22	0.18	0.19	0.18
PLE-PME	0.47	0.70	—	0.55	0.30	0.32	0.35	0.33	0.23	0.42	0.25	0.30
PME-PME	0.25	0.32	—	0.38	0.20	0.20	0.17	0.18	0.20	0.25	0.17	0.24
ALE-AME	0.11	0.16	—	0.15	0.03	0.05	0.06	0.08	0.06	0.08	0.08	0.10
AME-AME	0.17	0.20	—	0.19	0.11	0.13	0.06	0.08	0.10	0.10	0.12	0.12

Table 2.—Leg measurements of *Trechaleoides keyserlingi* male in mm.

Leg segment	I	II	III	IV
Femur	9.5	9.75	7.5	9.5
Tibia-patella	13.0	13.0	9.5	12.3
Metatarsus	10.3	10.4	7.8	11.6
Tarsus	7.4	8.1	4.2	7.4
Total	40.2	41.25	29.0	40.8

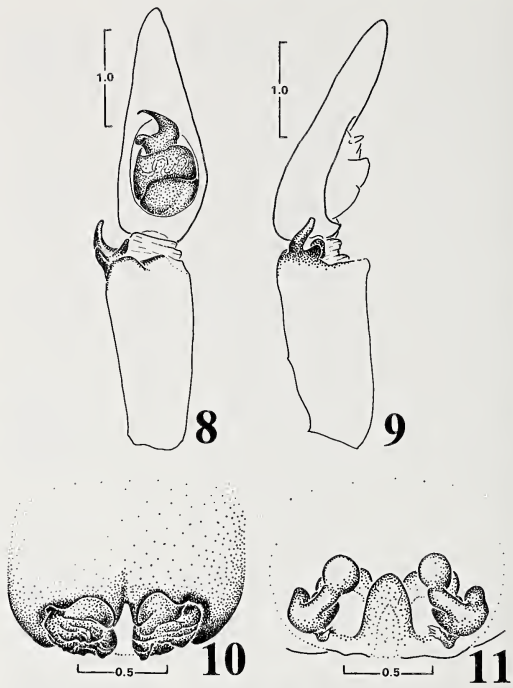
tified by Keyserling (1891) as *Trechalea longitarsis* (C.L. Koch 1848). However, the former recognized that the five retromarginal teeth of the chelicera and the shape of the epigynum clearly distinguish this species from the Koch species. It is these same characters, which, among others, also define the new genus, *Trechaleoides*.

Trechaleoides biocellata (Mello-Leitão 1926)
NEW COMBINATION
Figs. 3, 8–12

Trechalea biocellata Mello-Leitão 1926:3; Roewer 1954:142; Bonnet 1959:4678; Platnick 2004.

Type material.—Holotype female, Santa Catharina e Petropólis, Rio de Janeiro, Brazil, Fr. Thomaz Borgmeyer (MNRJ, presumed lost, not examined)

Material examined.—ARGENTINA: *Misiones*: Paulitz(?), 27°00′S, 55°00′W, 1954, Schiapelli & De Carlo?, 1 ♂ (MACN); no locality, November 1954, Scial. Corio?, 1 ♂ (MACN). BRAZIL: *Rio Grande do Sul*: Ituaba-Arroio do Tigre, 29°20′S, 53°06′W, 11 April 1978, A.A. Lise, 1 ♂ (MCN #7928); same locality, 12 April 1978, A.A. Lise, 1 ♀ (MCN #7978); same locality, 12 April 1978, C.J. Becker, 1 ♀, 1 juvenile (MCN #7904); same locality, 17 April 1978, A.A. Lise, 1 ♂, 5 juveniles (MCN #7978); Estreito Augusto César, Marcelino Ramos, 3 February, 1990, C. Martinazzo, 1 ♂, 1 juvenile (MCN #19532); Viamão, near Porto Alegre, 30°05′S, 51°02′W, 22 March 1975, A.A. Lise, 1 ♂ (MCN #02537); Garruchos São Borja, 28°11′S, 55°39′W, 10 December 1975, A.A. Lise, 3 ♂, 3 ♀ (MCN #3245); Arroio do Meio, Linha Alegre, 9 January 1985, A.A. Lise, 1 ♂ (MCN #13019). PARAGUAY: near Piribebuy, Arroyo Pirareta, 25°29′S, 57°03′W, 13 December 1956, C.J.D. Brown, 1 ♀ (MCZ).



Figures 8–11.—Genitalia of *Trechaleoides biocellata*. 8, 9. right palpus; 8. ventral view, 9. retrolateral view; 10, 11. female genitalia; 10. ventral view, 11. dorsal view.

Diagnosis.—This species is distinguished by characteristics of the genitalia. The pair of posterior projections of the epigynum are folded and not smooth, and the palpal tibia is approximately equal to the length of the cymbium.

Table 3.—Leg measurements of *Trechaleoides keyserlingi* female in mm.

Leg segment	I	II	III	IV
Femur	11.1	11.6	9.5	11.6
Tibia-patella	15.0	14.8	11.0	14.2
Metatarsus	10.8	10.1	9.0	13.3
Tarsus	8.0	8.1	5.0	8.5
Total	44.9	44.6	34.5	47.6

Table 4.—Leg measurements of *Trechaleoides biocellata* male in mm.

Leg segment	I	II	III	IV
Femur	11.9	12.6	9.3	12.1
Tibia-patella	16.5	16.7	11.5	15.1
Metatarsus	12.7	14.3	9.0	14.3
Tarsus	9.7	9.0	5.2	9.6
Total	50.8	52.6	35.0	51.1

Table 5.—Leg measurements of *Trechaleoides biocellata* female in mm. Leg I missing.

Leg segment	I	II	III	IV
Femur	—	13.5	10.5	13.2
Tibia-patella	—	17.0	12.6	15.3
Metatarsus	—	13.0	10.8	16.7
Tarsus	—	8.5	6.2	9.6
Total	—	52.0	40.1	54.8

Description.—*Male (Misiones, Argentina):* Carapace medium brown with wide submarginal light bands, marginal bands widening posteriorly, black in eye region, length 7.9, width 7.0. Sternum light, unmarked, length 4.2, width 3.7; labium reddish-brown, lighter at distal margin, length 1.57, width 1.30. Clypeus height 0.88, width 3.20. Anterior eye row slightly recurved, a cluster of bristles posterior to each PLE, eye measurements in Table 1. Cheliceral faces medium reddish-brown, each with a dark longitudinal band clothed with scattered light and dark hairs, five retromarginal teeth, subequal in size except smaller fifth one between first and third offset into the fang groove. Legs II-IV-I-III, measurements in Table 4, ventral macrosetae pairs on tibiae are I-4, II-4, III-3, IV-3. Color of legs medium brown, marked only with faint maculae on dorsum of each femur. Abdomen hairless above (probably rubbed), with distinct dorsal pattern, length 8.0. Palpus (Figs. 8, 9) tibia length approximately equal to length of cymbium, bulb t and st prominent, vd of ma small, flattened, rounded in outline, and not covering dd, ecd of rta prominent and angular.

Female (Paineiras, Brazil [substitute for holotype, see note below]): Carapace (Fig. 12) light brown with irregular submarginal lighter bands; irregular light marks between PE and thoracic groove, length 8.5, width 7.8. Sternum light yellow, unmarked, length 4.5, width 3.6; labium light brown, unmarked, length 1.80, width 1.60. Clypeus with faint darker marks beneath PLE and AE, height 0.86, width 3.5. Anterior eye row straight, eye measurements in Table 1. Chelicerae reddish brown, five retromarginal teeth, subequal in size with smallest one subproximal. Legs: IV-II-II (I missing), measurements in Table 5, yellow with irregular and indistinct darker marks on dorsal surfaces of femora, tibiae. Abdomen mid-dorsal dark band distinct with light marks at anterior and lateral edges; sides with irregular, parallel dark marks, venter unmarked, length 8.6. Pair of protuberances at posterior margin of epigynum (Figs. 10, 11) with irregular folds and creases, internal structures as for genus.

Variation.—Carapace length of males average 7.72 (7.2–8.6, n = 13) and of females 9.2 (7.2–11.0, n = 6). Average abdominal lengths equal 0.93 of carapace lengths in males and 0.97 in females. Dorsal pattern similar in both sexes with little variation noted.

Natural history.—See generic description.

Distribution.—Eastern tributaries of Rio Paraná in northern Argentina, southern Paraguay, and southern Brazil. Also some coastal drainages of southern Brazil (Fig. 3).

Remarks.—The female described above from the Museu Nacional do Rio de Janeiro, was identified by Mello-Leitão as *Trechalea biocellata* and is assumed to be the name bearer for the purposes of this report. I am reluctant to designate it as a neotype in view of the possibilities that the original holotype might be found in the future.

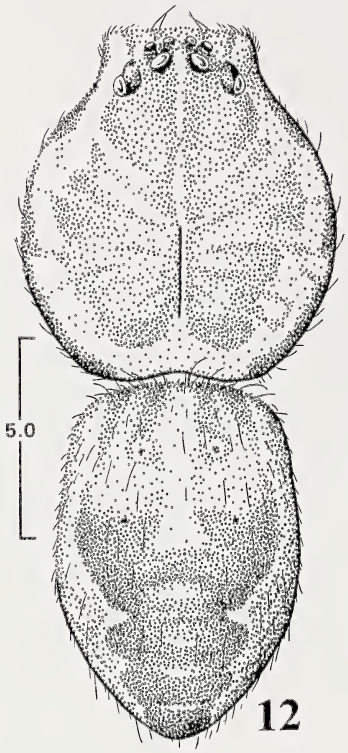
Paratrechalea new genus

Type species.—*Trechalea ornata* Mello-Leitão 1943.

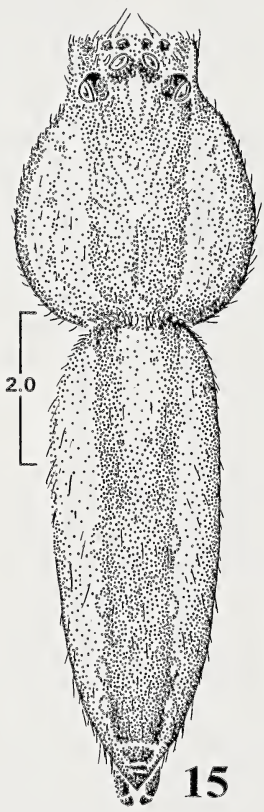
Etymology.—The feminine Latin generic name indicates the relationship with the genus *Trechalea*.

Diagnosis.—*Paratrechalea* can be distinguished from all other described genera of Trechaleidae (*sensu* Carico 1993) by a combination of characters. In the male palpus the ventral division (vd) of the median apophysis (ma) is flattened, rounded in outline, and greatly expanded to mostly obstruct the dorsal division including its guide (g). The epigynum is distinguished by the presence of a conspicuous external posterio-median scape. These are moderate-sized spiders with the carapace length ranging 3.3–3.8 except for the male of *P. wygodzinskyi* which is 5.2.

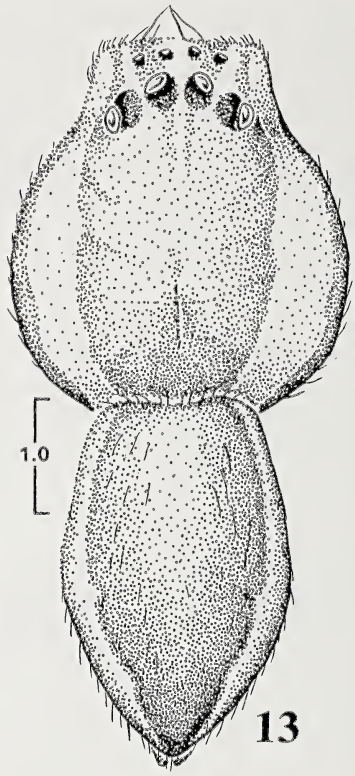
Description.—Carapace moderately low, cephalic area relatively distinct, AE row straight. Each basal segment of male chelicera swollen anteriorly with lateral carina on distal half (except *P. wygodzinskyi*); three promarginal teeth with center one largest, three, four or five retromarginal teeth, variable in size and interdistance. Leg lengths variable but III al-



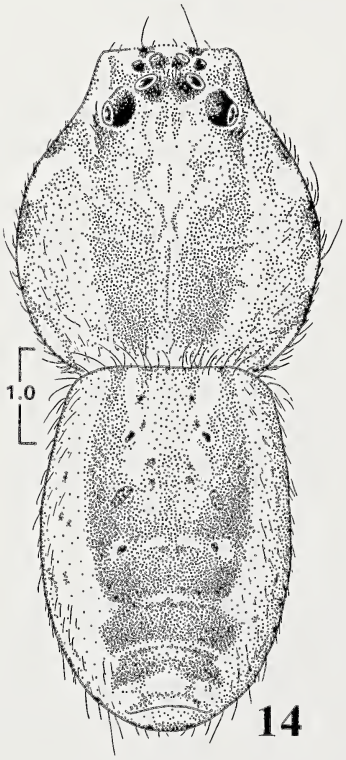
12



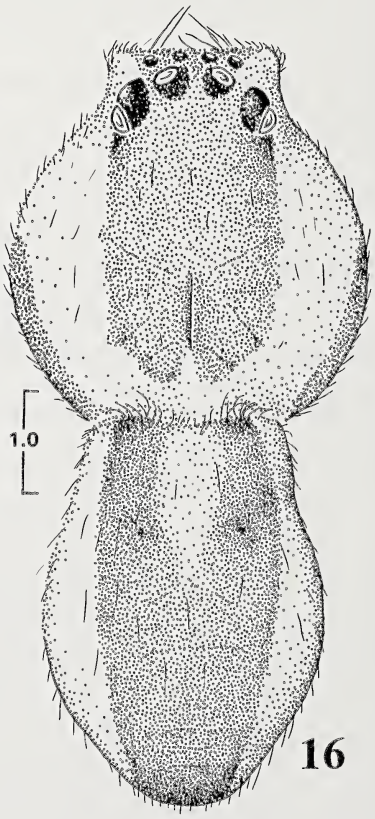
15



13



14



16

ways shortest while others often subequal, only tarsi flexible, all claws dentate.

Male palpal bulb (Fig. 1) with tip of distal, curved sickle-shaped dorsal division (dd) of median apophysis (ma) directed ventrad and obscured by broad, rounded ventral division (vd); retrolateral tibial apophysis (rta) arising distally and laterally from near the ventrodistal rim (vr) with ectal division (ecd) curved and ental division (end) partly surrounded by ventral cymbio-tibial membrane (vcm); tibial ventral rim (vr) of ventral protuberance (vp) folded over to create deep depression in ventral cymbio-tibial membrane (vcm). Nearly circular anterior field (af) of epigynum slightly convex, a single prominent posterio-median scape; dorsal aspect, on each side of the female genitalia (Fig. 21) with large, free, stalked, spermathecal head (hs); two diverticula arising from large common chamber (probably an extension of copulatory duct); large, hood-shaped structure (h) located posterio-medially; copulatory duct (cd) and fertilization duct (fd) arising from common chamber.

Natural history.—The aquatic habitat preference is suggested by the reference to "Arroyo" or "Rio" on some collection labels and is consistent with what is known of other trechaleid genera.

Distribution.—Found in South America southward from the Brazilian state of Mato Grosso through northern Argentina into Uruguay (Fig. 17).

Nomen dubium.—Unlike many of Mello-Leitão's species descriptions, the one for *T. limai* Mello-Leitão 1941 was relatively complete and was accompanied by drawings of the habitus and epigynum. Unfortunately the epigynum drawing was not diagnosable at either the generic or species level. The habitus was helpful however and when combined with the description, it is possible to determine the genus with some confidence. Specifically this decision is based upon body length, number of macrosetae pairs on the tibiae, relative length of the legs, and geographic location. Therefore, I believe that *T. limai* is a member of the genus *Paratrechalea*. Because of the inability to determine the relationship of this species to others in the genus, I have determined that it should remain as a nomen dubium until and if the holotype is ever recovered.

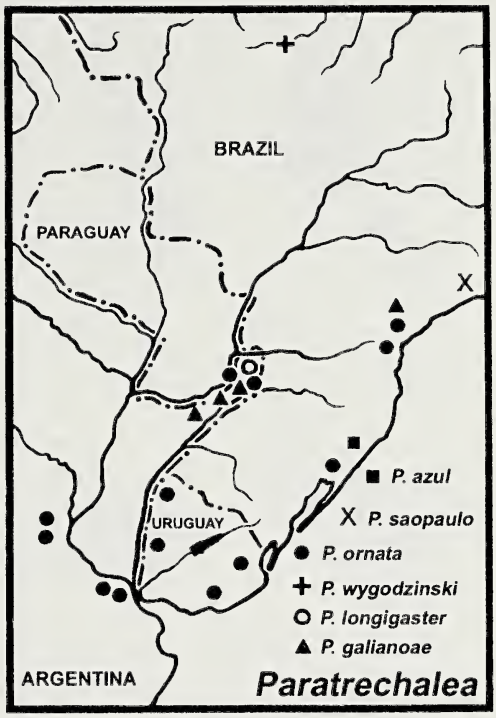


Figure 17.—Distribution of species of *Paratrechalea.*

Paratrechalea ornata (Mello-Leitão 1943)
NEW COMBINATION
Figs. 13, 14, 17–21

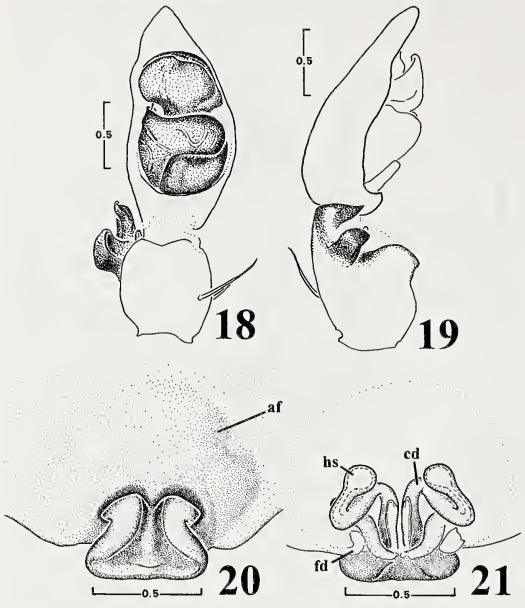
Trechalea ornata Mello-Leitão 1943:107, fig. 7; Roewer 1954:143; Platnick 2004.

Type material.—Holotype female, Bosque Alegre, Córdoba, Argentina, 31°35′S, 64°34′W, January–March 1940, M. Birabén (MLP #15690, examined).

Material examined.—ARGENTINA: *Misiones*: Isla Maria, 27°00′S, 55°00′W, November 1954, Schiapella?, 1 ♀ (MACN); *Cordoba*: Santa Rosa, Dept. de Calamuchita,

←

Figures 12–16.—Dorsal patterns of species of *Trechaleoides* and *Paratrechalea*. 12. *T. biocellata* female; 13—16. *Paratrechalea*; 13, 14. *P. ornata*; 13. male; 14. female; 15. *P. longigaster* female; 16. *P. galianoae* female.



Figures 18–21.—Genitalia of *Paratrechalea ornata*. 18, 19. right palpus; 18. ventral view, 19. retrolateral view; 20, 21. female genitalia; 20. ventral view, 21. dorsal view. af = anterior field, cd = copulatory duct, fd = fertilization duct, hs = head of spermathecum.

32°04′S, 64°33′W, February 1952, M.J. Viana, 2 ♀ (MACN); *Buenos Aires*: Arroyo Pararito, Delta del Paraná, Partido do Tigre, 34°25′S, 58°35′W, 29 November 1953, A.O. Bachman, 1 ♂, 2 ♀, 7 juveniles (MACN); same locality, October 1954, A.O. Bachman, 3 ♀ (MACN); same locality, 1 November 1953, A.O. Bachman, 3 ♂, 6 ♀, 4 juveniles (MACN); same locality, 26 December 1953, A.O. Bachman, 2 ♀ (MACN), 8 March 1953, A.O. Bachman, 1 ♀,(MACN); same locality, 18 October 1953, A.O. Bachman, 2 ♂, 7 juveniles (MACN); Arroyo, Carancho, Delta del Paraná, 36°12′S, 58°10′W, 6 January 1952, A.O. Bachman, 3 ♀ (MACN); Arroyo Correa, near San Antonio River, Delta del Paraná, Partido de Tigre, 34°25′S, 58°35′W, 2 March 1951, A.O. Bachman, 1 ♀ (MACN); Arroyo de las Moras, Delta del Paraná, Partido de Tigre, 34°25′S, 58°35′W, 3 February 1955, A.O. Bachman, 3 ♀ (MACN). BRAZIL: *Paraná*: Rio Bronco do Sul, 4°10′N, 60°47′W, 16 April 1987, A.D. Brescovit, 1 ♀ (MCN #17153); *Rio Grande do Sul*: Caxias do Sul, Áqua Azul, 27°23′S, 52°25′W, 15 January 1975, A.A. Lise, 1 ♀ (MCN). URUGUAY: *Treinta-y-Tres*: Arroyo Yerbal, 33°19′S, 54°42′W, 7 January 1963, Gambardella, 33°19′S, 54°42′W, 1 ♀ (MNHN); *Paysandú*: Santa Rita, R. Uruguay, 8 November 1955, collector unknown, 1 ♀ (MNHN); *Salto*, Rio Arapey, 30°55′S, 57°49′W, 13 December 1954, collector unknown, 1 ♀ (MNHN); *Maldonado*: Sa. De las Ánimas, 34°42′S, 55°19′W, 18 May 1989, R. Capocasale, F. Costa, 1 ♂, 1 ♀ (MNHN).

Table 6.—Leg measurements of *Paratrechalea ornata* male in mm.

Leg segment	I	II	III	IV
Femur	4.0	4.2	3.3	4.5
Tibia-patella	5.5	5.6	4.0	5.7
Metatarsus	4.2	4.2	3.0	5.2
Tarsus	2.2	2.4	1.5	2.6
Total	15.9	16.4	11.8	18.0

Diagnosis.—This species is distinguished by the small body size and details of the genitalia. The broad median scape of the epigynum has a median concavity. The male palpal tibia is approximately half the length of the cymbium but with a large rta. On the palpal bulb the vd of the ma is much expanded so that the tip of the g is out of view from the ventral side.

Description.—*Male (Argentina, Arroyo de la Moras, Provincia Buenos Aires):* Carapace (Fig. 13) moderately high, cephalic area not elevated, medium brown with wide submarginal light band, marginal bands widening posteriorly, black in eye region, length 3.3, width 3.0. Sternum light, unmarked, length 1.72, width 1.80; labium reddish-brown, lighter at distal margin, length 0.60, width 0.60. Clypeus height 0.30, width 1.70. Anterior eye row slightly recurved, eye measurements in Table 1. Cheliceral faces swollen, glabrous, yellowish, lateral longitudinal carinae present, four retromarginal teeth subequal in size except smallest subproximal. Legs IV-II-I-III,

Table 7.—Leg measurements of *Paratrechalea ornata* female in mm.

Leg segment	I	II	III	IV
Femur	4.3	4.5	3.6	5.0
Tibia-patella	5.6	5.7	4.0	5.9
Metatarsus	4.1	4.1	3.1	5.3
Tarsus	2.3	2.2	1.5	2.4
Total	16.3	16.5	12.2	18.6

measurements in Table 6, ventral macrosetae pairs on tibiae are I-5, II-4, III-3, IV-3. Color of legs light brown, unmarked. Abdomen with wide median dark band, narrow light line on each lateral margin, length 3.6. Palpus (Figs. 18, 19) tibia approximately half length of cymbium with end cupped of very prominent rta; bulb t and st prominent, vd of ma large, flattened, rounded, and covering most of dd including g.

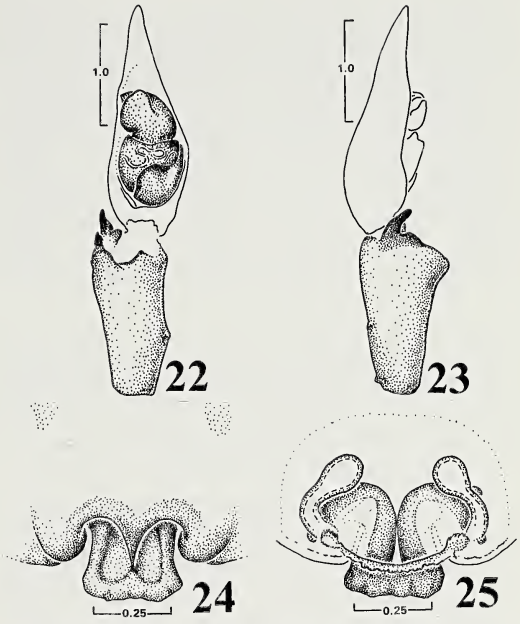
Female (holotype): Carapace (Fig. 14) moderately high, cephalic area not elevated, color pattern with a broad, dark median band, light submarginal bands with irregular areas of white hair, margin with short marginal dark areas, length 3.5, width 3.2. Sternum light, unmarked, length not determined, width 1.40; labium medium brown, lighter at distal margin, length 0.65, width 0.56. Clypeus height 0.27, width 1.38. Anterior eye row straight, eye measurements in Table 1. Chelicerae each with dark longitudinal band on base; three promarginal teeth on left side, two on the right, four retromarginal teeth on both sides. Legs IV-II-I-III, measurements on Table 7, indistinct grey maculae present except on tibia III, tibial macrosetae not observed. Abdomen median dark band with irregular margins, lateral areas with scattered small dark maculae, venter unmarked, length 4.0. Median scape of epigynum (Figs. 20, 21), wider than long, prominent and widened posteriad and with a single medial depression, internal structures as for genus.

Variation.—Carapace length of males average 3.5 (3.3–3.8, n = 10) and of females 3.65 (2.8–4.5, n = 30). Average abdomen lengths equal 1.05 of carapace lengths in males and 1.18 in females. Dorsal pattern in both sexes ranges from a distinct median dark band with lateral light bands (Fig. 13) to a much more diffuse pattern (Fig. 14). The diameters of three egg sacs measuring 5.5, 6.0, and 5.1 were recorded.

Natural history.—See generic description.

Distribution.—Southward from the southern Brazilian state of Paraná to northern Argentina and Uruguay (Fig. 17).

Remarks.—This species is not to be confused with *Hesydrus ornatus* Mello-Leitão 1941. The type of the latter species is a small spiderling and is treated as a *nomen dubium* in a revision of the genus *Hesydrus* (Carico 2005).



Figures 22–25.—Genitalia of *Paratrechalea* species. 22, 23. right palpus of *P. wygodzinskyi*; 22. ventral view; 23. retrolateral view; 24, 25. female genitalia of *P. longigaster*, 24. ventral view, 25. dorsal view.

Paratrechalea wygodzinskyi (Soares & Camargo 1948)
Figs. 17, 22, 23

Trechalea wygodzinskyi Soares & Camargo 1948: 358, figs. 6, 7; Roewer 1954:143; Carico 1993: 237 (non *Trechalea*); Platnick 2004.

Type material.—Holotype male, Chavantina, Mato Grosso, Brazil, 14°40′S, 52°21′W, October 1946, H. Sick (MZUSP, #E.788, C.1293, examined)

Diagnosis.—The pedipalp is distinguished from *P. ornata* by the relatively elongated tibia which is approximately the length of the cymbium and the small rta.

Description.—*Male (holotype):* Carapace low, cephalic area not elevated, light with a narrow marginal band and indistinct darker central area, dark lines between each AME and clypeus margin, length 5.2, width 4.6. Sternum light with a pair of dark spots in posterior half, length 2.52, width 2.70; labium reddish-brown, length 0.46, width 0.41. Clypeus height 0.72, width 1.93. Anterior eye row straight, eye measurements in Table 1. Chelicerae face reddish brown with indistinct darker areas in distal half, without lateral carina or

Table 8.—Leg measurements of *Paratrechalea wygodzinskyi* male in mm. Leg I missing.

Leg segment	I	II	III	IV
Femur	—	8.3	6.7	8.5
Tibia-patella	—	11.9	7.7	9.8
Metatarsus	—	9.7	7.1	11.7
Tarsus	—	4.6	3.8	5.3
Total	—	34.5	25.3	35.3

Table 9.—Leg measurements of *Paratrechalea longigaster* female in mm. Leg I missing.

Leg segment	I	II	III	IV
Femur	—	5.0	3.5	6.0
Tibia-patella	—	6.5	4.0	6.3
Metatarsus	—	4.6	3.7	5.8
Tarsus	—	2.4	1.5	2.7
Total	—	18.5	12.7	20.8

frontal enlargement on basal segment, four subequal retromarginal teeth. Legs IV-II-III (I missing), measurements in Table 8, ventral macrosetae pairs on tibiae are II-5, III-4, IV-4. Color of legs light with dark maculae especially on ventral side of femora, less so on distal segments. Abdomen light with striated patterns of pigment laterally and above, particularly dorsolaterally except for pair of light areas at two-thirds of length, light ventrally but darker laterally, length 5.0. Palpus (Figs. 22, 23) tibia approximately 0.8 length of cymbium, bulb t and st prominent, vd of ma large, flattened, rounded, and covering most of the dd but leaving g visible; ecd of rta narrow and curved ventrally, end very low.

Female: Unknown.

Natural history.—Unknown.

Material examined and distribution.—Known only from the type specimen collected in Mato Grosso, Brazil (Fig. 17).

Paratrechalea longigaster new species
Figs. 15, 17, 24, 25

Type material.—Holotype female, Santa Maria, Misiones, Argentina, 27°00′S, 55°00′W, 1956, M.J. Viana (MACN).

Etymology.—The name means "long stomach" and is derived from Latin.

Diagnosis.—This species is characterized by the details of the median epigynal scape which includes a pair of deep depressions laterally separated by a wedge-shaped elevation. Additionally, there are three retromarginal teeth, and the abdomen, when compared with other species, is narrow and elongated, about twice its width.

Description.—*Female (holotype):* Carapace (Fig. 15) low, cephalic area not elevated, color pattern with a broad, dark median band, light submarginal bands with irregular maculae, narrow dark margin, length 3.8, width 3.2. Sternum light, median longitudinal macula, three small maculae each side, length 1.95, width 1.80; labium medium brown, lighter at distal margin, length 0.30, width 0.30. Clypeus height 0.25, width 1.50. Anterior eye row straight, eye measurements in Table 1. Chelicerae each with dark longitudinal band on base; three promarginal teeth, three retromarginal teeth. Legs IV-II-III (leg I missing), measurements on Table 9, color light with small dark spots on ventral side of femora. Abdomen median dark band bordered laterally with three light spots, lateral sides indistinctly marked, venter with numerous small dark spots, length 6.50. Median scape of epigynum (Figs. 24, 25) prominent, pair of deep depressions laterally separated by median, wedge-shaped elevation, internal structures as for genus.

Natural history.—Unknown.

Material examined and distribution.—Known only from the type specimen collected in Argentina (Fig. 17).

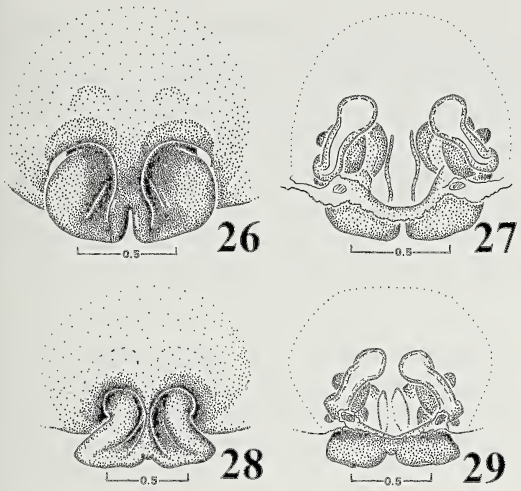
Paratrechalea galianoae new species
Figs. 16, 17, 26, 27

Type material.—Holotype female, General M. Belgrado, Misiones, Argentina, 27°00′S, 55°00′W, January 1966, M.E. Galiano (MACN).

Other material examined.—ARGENTINA: *Misiones*, General Manuel Belgrado, January 1966, M.E. Galiano, 1♀ (MACN), Tobuna, February 1959, W. Partridge, 1♀ (MACN). BRAZIL: *Paraná*, Rio Branco do Sul, 16 April 1987, A.D. Brescovit, 1♀ (MCN #17153). (Fig. 17).

Etymology.—The name is in honor of the collector, the late M.E. Galiano, in recognition of her contributions to arachnology and in appreciation for her aid to the author in this project.

Diagnosis.—This species is characterized by the details of the epigynum which include a unique Y-shaped median ridge on the round-



Figures 26–29.—Female genitalia of *Paratrechalea* species. 26, 27. *P. galianoae*; 26. ventral view, 27. dorsal view; 28, 29. *P. azul*; 28. ventral view, 29. dorsal view.

ed scape with a deep cleft found at the posterio-median margin. Additionally, the carapace and abdomen have a broad, median dark band which is flanked by a light submarginal band on the carapace with white hairs.

Description.—*Female (holotype):* Carapace (Fig. 16) moderately high, cephalic area not elevated, color pattern with a broad, dark median band, light submarginal bands with white hairs, narrow dark margin along posterior half, length 3.8, width 3.5. Sternum light, unmarked, length 1.95, width 1.80; labium medium brown, lighter at distal margin, length 0.66, width 0.70. Clypeus height 0.33, width 1.62. Anterior eye row slightly recurved, eye measurements in Table 1. Chelicerae each with faint longitudinal band on base; three promarginal teeth, four retromarginal teeth. Legs IV-II-I-III, measurements in Table 10, ventral macrosetae pairs on tibiae are I-4 II-4, III-3, IV-3, color light and unmarked. Abdomen with distinct median dark band, sides light and unmarked, venter medium with indistinct mottling, length 3.7. Rounded scape of epigynum (Figs. 26, 27) prominent, with a median elevation extending posteriad from the af terminating in a Y-shaped ridge on the posterior margin around a deep cleft, internal structures as for genus.

Variation.—Carapace length ranges 3.0–3.8 among three females. Dorsal pattern may be with dark median band (Fig. 16) or diffuse without distinct bands.

Table 10.—Leg measurements of *Paratrechalea galianoae* female in mm.

Leg segment	I	II	III	IV
Femur	5.0	5.3	3.8	5.7
Tibia-patella	6.7	6.7	4.4	6.3
Metatarsus	6.5	6.5	3.6	6.2
Tarsus	2.5	2.5	1.7	3.1
Total	20.7	21.0	13.5	21.3

Paratrechalea azul new species
Figs. 17, 28, 29

Type material.—Holotype female, Água Azul, Caixas do Sul, Rio Grande do Sul, Brazil, 27°23′S, 52°25′W, 15 January 1975, A.A. Lise (MCN #02551).

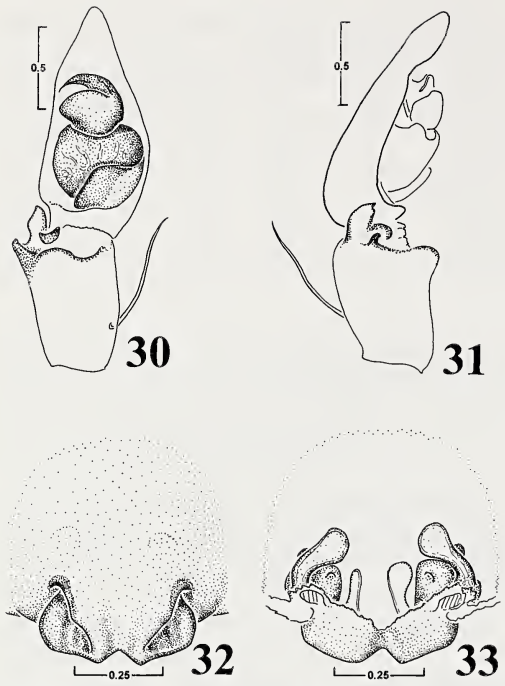
Etymology.—The name is a noun in apposition suggested by the name of the type locality.

Diagnosis.—This species is characterized by the details of the epigynum which has a pronounced lateral flare to the posterior, wider-than-long scape and a median indention on the posterio-median margin. The body is distinctly larger than females of other species measured by the carapace length. Also, the legs are proportionally longer as determined by the ratio of carapace length/leg IV length, e.g., 6.0 vs. 5.4 average (5.3–5.6) for other species.

Description.—*Female (holotype):* Carapace moderately high, cephalic area not elevated, color pattern with a diffuse arrangement of mottling, length 5.1, width 4.5. Sternum light with faint maculae near base of femora, length 2.50, width 2.4; labium light, lighter at distal margin, length 0.88, width 0.85. Clypeus height 0.41, width 2.04. Anterior eye row slightly recurved to straight, eye

Table 11.—Leg measurements of *Paratrechalea azul* female in mm.

Leg segment	I	II	III	IV
Femur	7.0	7.4	6.0	8.0
Tibia-patella	9.3	9.7	7.0	9.5
Metatarsus	7.4	7.1	5.3	9.0
Tarsus	4.0	4.0	2.4	4.3
Total	27.7	28.2	20.7	30.8



Figures 30–33.—Genitalia of *Paratrechalea saopaulo*. 30, 31. right palpus; 30. ventral view, 31. retrolateral view; 32, 33. female genitalia; 32. ventral view, 33. dorsal view.

measurements in Table 1. Chelicerae each without distinct marks on base; three promarginal teeth, four retromarginal teeth. Legs IV-II-I-III, measurements in Table 11, ventral macrosetae pairs on tibiae are I-4 II-4, III-3, IV-3, color light with indistinct maculae. Abdomen with diffuse arrangement of mottling, sides light and unmarked, venter medium without mottling, length 5.6. Scape of epigynum (Figs. 28) prominent, wider than long, with a flared posterior scape extending posteriad from the af terminating with an indentation on posteriomedian margin, median longitudinal ridge; internal structures as for genus (Fig. 29).

Distribution.—Known only from the type specimens collected in Brazil (Fig. 17).

Paratrechalea saopaulo new species
Figs. 17, 30–33

Type material.—Holotype male, São Paulo, São Paulo, Brazil, 22°00′S, 49°00′W 1897, Moenkhouse (PMNH). Paratypes: 9 males, 10 females same data as holotype (PMNH).

Etymology.—The name is a noun in apposition suggested by the name of the type locality.

Table 12.—Leg measurements of *Paratrechalea saopaulo* male in mm.

Leg segment	I	II	III	IV
Femur	4.3	4.2	3.4	4.8
Tibia-patella	6.2	5.9	4.0	5.5
Metatarsus	4.6	4.5	3.3	5.5
Tarsus	2.5	2.3	1.5	2.5
Total	17.6	16.9	12.2	18.3

Diagnosis.—This species is distinguished by the small body size and details of the genitalia. Externally, the median division of the epigynum separates two posterio-lateral divisions and has a furrow along the posterior edge. The male palpal tibia is approximately equal the length of the cymbium. The rta ental division is a small, dark, sclerotized projection while the ectal division is larger, acute, white and lightly sclerotized. On the palpal bulb the vd of the ma is much expanded and rounded while the tip of the g is visible from the ventral side.

Description.—*Male (holotype):* Carapace moderate high, cephalic area not elevated, color pattern faded due to age but faintly resembles Fig. 15, length 3.8, width 3.2. Sternum light, central dark macula, length 2.1, width 1.6; labium light reddish-brown, lighter at distal margin, length 0.63, width 0.54. Clypeus height 0.28, width 1.60. Anterior eye slightly recurved, eye measurements in Table 1. Chelicerae faces swollen, glabrous, yellowish, lateral longitudinal carinae present, three retromarginal teeth subequal. Legs IV-I-II-III, measurements in Table 12, ventral macrosetae pairs on tibiae are I-5, II-5, III-3, IV-3. Color of legs light with small maculae at the bases of most macrosetae. Abdomen color faded from age but similar to Fig. 15, length 4.7. Palpus (Figs. 30, 31) tibia approximately equal to length of cymbium, cupped end of

Table 13.—Leg measurements of *Paratrechalea saopaulo* female in mm.

Leg segment	I	II	III	IV
Femur	4.1	4.2	2.5	5.2
Tibia-patella	5.6	5.5	3.7	5.3
Metatarsus	4.0	3.8	3.0	5.0
Tarsus	2.0	1.9	1.4	2.1
Total	15.7	15.4	10.6	17.6

prominent rta white, acute and ect a small dark projection; bulb t and st prominent; vd of ma large, flattened, rounded, and covering most of dd but g is prominent.

Female (Paratype): Carapace moderately high, cephalic area not elevated, color pattern as with male, length 3.8, width 3.3. Sternum light, small central macula, length 1.7, width 1.8; labium medium brown, lighter at distal margin, length 0.61, width 0.60. Clypeus height 0.42, width 1.60. Anterior eye row slightly recurved, eye measurements in Table 1. Chelicerae medium; three promarginal teeth, three retromarginal teeth equidistant and equal in size. Legs IV-I-II-III, measurements in Table 13, color as in male. Abdomen color as in male, length 5.3. Pair of protuberances at posterio-laterally on margin of epigynum continuous with median elevation (Fig. 32), median elevation widened anteriorly and with a medial furrow at posterior margin; internal parts (Fig. 33) as for genus.

Variation.—Carapace length of males average 3.6 (3.3–3.9, n =10) and of females 3.5 (3.3–3.9, n = 10). The diameters of two egg sacs measuring 4.8 and 5.3 were recorded. Egg sac structure is typical for the family but with upper valve arched higher.

Natural history.—Unknown.

Distribution.—Known only from the type series collected in Brazil composed of 10 males and 10 females (Fig. 17).

ACKNOWLEDGMENTS

Thanks are extended to the following persons and museums for the loan of specimens: R. Pinto da Rocha and J.L.M. Leme (MZUSP); H.W. Levi (MCZ); P.D. Hillyard and J. Beccaloni (BMNH); E.H. Buckup and A.A. Lise (MCN); the late M.E. Galiano (MACN); R.M. Capocasale (MNHN); C.F. Ituarte (MLP); A.B. Kury and R. Baptista (MNRJ); Estevam Luis Cruz da Silva (UFRGS); and C.L. Remington (PMNH). W.A. Sherwood helped with translation from Portuguese. Thanks also to N.A. Carico, E.L. Cruz da Silva, editors and reviewers who helped make important improvements.

LITERATURE CITED

Berkum, F.H. Van. 1982. Natural history of a tropical, shrimp-eating spider (Pisauridae). Journal of Arachnology 10:117–121.

Bonnet, P. 1959. Bibliographia Araneorum. Toulouse 2(5):4231–5058

Brescovit, A.D., J. Raizer & M.E.C. Amaral. 2000. Descriptions and notes on the genus *Paradossenus* in the Neotropical region (Araneae, Trechaleidae). Journal of Arachnology 28:7–15.

Carico, J.E. 1986. Trechaleidae: A "new" American spider family. P. 305. *In* Proceedings of the Ninth International Congress of Arachnology, Panama 1983. (W. G. Eberhard, Y. D. Lubin & B. C. Robinson, eds.). Smithsonian Institution Press, Washington, D.C..

Carico, J.E. 1993. Revision of the genus *Trechalea* Thorell (Araneae, Trechaleidae) with a review of the taxonomy of the Trechaleidae and Pisauridae of the Western Hemisphere. Journal of Arachnology 21:226–257.

Carico, J.E. 2005. Revision of the spider genus *Hesydrus* (Araneae, Lycosidae, Trechaleidae). Journal of Arachnology 33:783–794.

Cambridge, F.O.P. 1903. On some new species of spiders belonging to the families Pisauridae and Senoculidae; with characters of a new genus. Proceedings of the Zoological Society of London 1903:151–168.

Coddington, J.A. & H.W. Levi. 1991. Systematics and evolution of spiders (Araneae). Annual Review of Ecology and Systematics 22:562–592.

Griswold, C.E. 1993. Investigations into the phylogeny of the lycosoid spiders and their kin (Arachnida, Araneae, Lycosoidea). Smithsonian Contributions to Zoology 539:1–39.

Keyserling, E. 1891. Die Spinnen Americas. Brasilianische Spinnen, Nürnberg 3:1–278.

Mello-Leitão, C.F. 1926. Algumas aranhas do Brasil Meridional. Boletim Museu Nacional do Rio de Janeiro 2(5):3–4.

Mello-Leitão, C.F. 1941a. Aranhas do Paraná. Arquivos do Instituto Biologico do São Paulo 11(30):235–257.

Mello-Leitão, C.F. 1941b. Las arañas de Córdoba, La Rioja, Calamarca, Tucumán, Salta y Jujuy colectadas por los Profesores Birabén. Revista Museo La Plata 2:99–198.

Mello-Leitão, C.F. 1943. Arañas nuevas de Mendoza, La Rioja y Cordoba coligidas por el Prof. M. Biraben. Revista Museo de La Plata 3(20): 101–121.

Petrunkevitch, A. 1911. A synonymic index-catalogue of spiders of North, Central, and South America with all adjacent islands, Greenland, Bermuda, West Indies, Terra del Fuego, Galapagos, etc. Bulletin of the American Museum of Natural History 29:1–791.

Platnick, N.I. 2004. The World Spider Catalog, Version 4.5. American Museum of Natural History, online at http://research.amnh.org/entomology/spiders/catalog/index.html

Roewer, C.F. 1954. Katalog der Araneae, vol. 2a. Institut Royal des Sciences Naturelles de Belgique, Bruxelles.

Sierwald, P. 1989. Morphology and ontogeny of female copulatory organs in American Pisauridae, with special reference to homologous features (Arachnida: Araneae). Smithsonian Contributions to Zoology 484:1–24.

Sierwald, P. 1990. Morphology and homologous features in the male palpal organ in Pisauridae and other spider families, with notes on the taxonomy of Pisauridae (Arachnida: Araneae). Nemouria, Occasional Papers of the Delaware Museum of Natural History 35:1–59.

Sierwald, P. 1993. Revision of the spider genus *Paradossenus*, with notes on the family Trechaleidae and the subfamily Rhoicininae (Araneae: Lycosoidea). Revue Arachnologique 10(3):53–74.

Sierwald, P. 1997. Phylogenetic analysis of pisaurine nursery web spiders, with revisions of *Tetragonophthalma* and *Perenethis* (Araneae, Lycosoidea, Pisauridae). Journal of Arachnology 25: 361–407.

Simon, E. 1890. Etudes arachnologiques. 22e Mémoire. XXXIV. Etude sur les Arachnides de l'Yemen. Annales Société Entomologique de France 10:77–124.

Soares, B.A.M. & H.F.A. Camargo. 1948. Aranhas coligidas pela fundação Brasil-Central (Arachnida-Araneae). Boletim do Museu Paraense de Historia Naturale Ethnographia. 10:355–409.

Manuscript received 8 December 2003, revised 26 August 2004.

2005. The Journal of Arachnology 33:813–819

LIVING WITH THE ENEMY: JUMPING SPIDERS THAT MIMIC WEAVER ANTS

Ximena J. Nelson[1], Robert R. Jackson[1], G.B. Edwards[2] and **Alberto T. Barrion[3]**: [1]Department of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch, New Zealand E-mail: robert.jackson@canterbury.ac.nz; [2]Florida State Collection of Arthropods, Division of Plant Industry, Gainesville, Florida 32614-7100, U.S.A.; [3]Entomology Division, International Rice Research Institute, PO Box 3127, Makati Central Post Office, 1271 Makati City, Philippines

ABSTRACT. Ants prey on salticids, and encounters with weaver ants (*Oecophylla smaragdina* (Fabricius 1775)) appear to be especially dangerous for many salticids. In the Philippines, *Myrmarachne assimilis* Banks 1930 is a salticid that mimics *Oecophylla smaragdina*. We tested for the abilities of four categories of salticids, plus *M. assimilis*, to survive in the proximity of weaver ants. The four categories were: (1) myrmecomorphic (ant-like species other than *M. assimilis*); (2) myrmecophagic (ant-eating species); (3) myrmecophilic (a species that is either myrmecophagic nor myrmecophagic, but is known to associate with ants) and (4) ordinary (species that are neither ant-like nor ant-eating, and are not known to associate with ants). The hypothesis investigated here is that *M. assimilis* has, compared with other salticids, especially pronounced ability to survive in close proximity with this particular ant species. The individual salticids used in our experiments had not had previous contact with weaver ants or any other ants. When confined with groups of 10 weaver ants, the myrmecomorphic, myrmecophagic and myrmecophilic species survived significantly more often than ordinary salticids, but *Myrmarachne assimilis* survived significantly more often than all other categories. When kept with groups of 20 ants, there was a proportional decrease in the number of salticids that survived within each salticid category. However, few salticids survived when confined with groups of 40 ants, regardless of category.

Keywords: Salticidae, mimicry, predation, myrmecomorphy, myrmecophily

In the Philippines, *Diacamma rugosum* (Le Guillou 1842) (previously known as *D. vagans*), *Dolichoderus thoracicus* Stitz 1925 (previously known as *D. bituberculatus*), *Oecophylla smaragdina* (Fabricius 1775), *Odontomachus* sp., *Polyrachis* spp. and *Solenopsis geminata* (Fabricius 1804) are ants that prey on jumping spiders (Salticidae) (Nelson et al. 2004). In an earlier laboratory study (Nelson et al. 2004), four categories of salticids were tested with these same ant species to measure their ability to survive in the presence of ants: (1) myrmecophagic species (i.e., species that select ants as preferred prey; see Li & Jackson 1996), (2) myrmecomorphic species (i.e., species that resemble ants; see Jackson & Willey 1994; Cushing 1997), (3) myrmecophilic species (i.e., a salticid species that is neither myrmecophagic nor myrmecomorphic, but known to associate with ants; see Nelson et al. 2004) and (4) ordinary species (i.e., species that are not known to associate with ants and are neither ant eaters nor ant mimics; see Jackson & Pollard 1996). These tests were carried out in small cages (diameter 90 mm) by putting one salticid together with one or with five ants per cage and then measuring how many spiders survived after 10 h with the ants. The ordinary salticids had the least success at surviving these tests, suggesting that ant eaters, ant mimics and ant associates have generalized adaptations that enhance their abilities to survive in the presence of a variety of ants, at least when the number of ants is small.

Here we investigate the ability of a variety of salticids to survive in the presence of numerous ants in large cages and we focus on a particular ant species, *Oecophylla smaragdina*. There are two species in the genus *Oecophylla*, *O. smaragdina* in tropical Asia and Australasia and *O. longinoda* (Latreille 1802) in tropical Africa. Known as 'weaver ants', these two species often dominate local arboreal habitats (Vanderplank 1960; Lokkers

1986) where they make nests by spinning leaves together with silk. The larvae of *Oecophylla* secrete the silk (Doflein 1905), but the workers determine where the silk goes. By carrying the larvae about and moving them across locations in need of silk, the major workers of *Oecophylla* use the larvae as nest-building tools (Hölldobler & Wilson 1977a). Minor workers generally remain inside the nests, whereas the more numerous major workers leave the nests and function as aggressive predators and soldiers for the colony (Hölldobler & Wilson 1977b, 1978; Hölldobler 1983). A single *Oecophylla* colony, with one queen, is typically spread across numerous nests and sometimes more than one tree (Hölldobler & Wilson 1977c). As many as half a million workers may live in a single colony (Hölldobler 1983).

Different species of *Myrmarachne* resemble different ant species (Wanless 1978; Edmunds 2000), but *Myrmarachne assimilis* is unique among the Philippine species studied because it alone resembles *O. smaragdina*. For *Myrmarachne*, myrmecomorphy appears to function primarily as Batesian mimicry, where predators that avoid the model (the ant) also avoid the mimic (the salticid). However, Batesian mimics of ants may be forced to 'walk a tightrope', needing to 'live with the enemy'. They need to be close to the model for safety from other predators but at the same time they need to avoid becoming the model's prey (see Reiskind 1970; Edmunds 1974; Elgar 1993; Oliveira 1988). Weaver ants appear to be exceptionally aggressive, yet *M. assimilis* routinely keeps close company with weaver-ant colonies in nature.

Cuticular hydrocarbons are used by many ants for distinguishing between nestmates and non-nestmates (Hölldobler & Wilson 1990; Thomas et al. 1999; Wagner et al. 2000). Chemical mimicry of ants has been reported for the salticid *Cosmophasis bitaeniata* (Keyserling 1882) (Allan & Elgar 2001; Allan et al. 2002; Elgar & Allan 2004). Perhaps in the field *M. assimilis* uses some form of chemical communication to avoid predation by *O. smaragdina*. However, the objective of the present study was not to investigate a hypothesis about mimics exploiting the nest-mate recognition system of *O. smaragdina*. Instead, our objective was to investigate whether *M. assimilis* might have evolved adaptations that make it especially proficient at surviving in the presence of its model even in the absence of opportunity to acquire nest-mate cues. The salticids we used were from laboratory cultures and could not have acquired any host-specific cuticular hydrocarbons by feeding on ants or through direct contact with ants (see Elgar & Allan 2004) because the individuals we used had never encountered ants before being tested. We tested different types of salticids in the laboratory by confining them in cages with groups of weaver-ants, our prediction being that *M. assimilis* would survive often more than other salticids, including other myrmecomorphs that do not specifically mimic weaver ants.

METHODS

In the Philippines, our study site was the vicinity of Los Baños (Laguna Province, Luzon, 14°10′ N 121°14′ E), including a rain forest habitat at Mt. Makiling. Laboratory tests were performed at the International Rice Research Institute (IRRI) in Los Baños. When needed, we collected weaver ants from the field, but all salticids used in experiments came from laboratory cultures and none had prior experience with ants of any species. No individual salticid nor any individual ant group was tested more than once. Tests were aborted whenever two or more ants died during testing, but this rarely happened. For each salticid species, a series of tests was carried out using both mature females and juveniles. Body length of the adult salticids varied (see Nelson et al. 2004) and juveniles were used when they were 3mm long. Salticid maintenance procedures were the same as in earlier spider studies (Jackson & Hallas 1986).

All tests began at c. 0800 hours and lasted 10 h (laboratory photoperiod 12L:12D, lights on at 0700 hours) and consisted of placing a single salticid in a cage with either 10, 20 or 40 ants. At the end of each test, we counted how many salticids were still alive. Our objective in this study was only to compare the percent survival for the different groups of salticids. Latency to attack and the behavior of ants and spiders during the tests were not recorded. Survival data were analyzed using tests of independence (Sokal & Rohlf 1995), with Bonferroni adjustments being applied whenever multiple comparisons were made using the same data sets (see Rice 1989).

Table 1.—Salticids used in tests with ant workers in laboratory. Ordinary salticid: species that are not known to associate with ants and are neither ant eaters nor ant mimics. Myrmecophagic salticid: species that select ants as preferred prey. Myrmecomorphic salticid: species that resemble ants. Myrmecophilic salticid: a salticid species that is neither myrmecophagic nor myrmecomorphic, but known to associate with ants.

Species of Salticidae	Category
Bavia sexpunctata (Doleschall 1959)	Ordinary salticid
Chalcotropis gulosa (Simon 1902)	Myrmecophagic
Chalcotropis luceroi Barrion & Litsinger 1995	Myrmecophagic
Cosmophasis estrellaensis Barrion & Litsinger 1995	Ordinary salticid
Epeus hawigalboguttatus Barrion & Litsinger 1995	Ordinary salticid
Harmochirus brachiatus (Thorell 1877)	Ordinary salticid
Heratemita alboplagiata (Simon 1899)	Ordinary salticid
Lagnus sp.	Ordinary salticid
Mantisatta longicauda Cutler & Wanless 1973	Ordinary salticid
Menemerus bivittatus (Dufour 1831)	Ordinary salticid
Myrmarachne assimilis Banks 1930	Myrmecomorphic
Myrmarachne bakeri Banks 1930	Myrmecomorphic
Myrmarachne bellicosa (G. & E. Peckham 1892)	Myrmecomorphic
Myrmarachne bidentata Banks 1930	Myrmecomorphic
Myrmarachne maxillosa (C. L. Koch 1846)	Myrmecomorphic
Myrmarachne nigella Simon 1901	Myrmecomorphic
Orthrus bicolor Simon 1900	Ordinary salticid
Phintella piatensis Barrion & Litsinger 1995	Myrmecophilic
Portia labiata (Thorell 1887)	Ordinary salticid
Plexippus petersi (Karsch 1878)	Ordinary salticid
Siler semiglaucus Simon (1901)	Myrmecophagic
Telamonia masinloc Barrion & Litsinge 1995r	Ordinary salticid
Thiania sp.	Ordinary salticid
Xenocytaea sp.	Myrmecophagic

We tested 24 salticid species (Table 1), all of which were also used in the earlier study (Nelson et al. 2004). Statistical analysis was based on the *a priori* categories from the earlier study, plus one additional *a priori* category (mimic of the weaver ant, *M. assimilis*). Other than *M. assimilis*, these categories were: myrmecomorphic salticids (*Myrmarachne* species other than *M. assimilis*); myrmecophagic salticids, ordinary salticids and a myrmecophilic salticid (Table 1). Voucher specimens of all species have been deposited in the IRRI Taxonomy Laboratory in Los Baños and in the Florida State Collection of Arthropods in Gainesville.

The testing apparatus was a cylindrical plastic cage (diameter & height *c.* 200 mm) with a ventilation hole (diameter 10 mm; covered by fine-mesh metal screening) centered at the top, and with four cork holes (diameter of each, 10 mm) spaced evenly around the top of each cage, each hole was 10 mm from the edge of the cage top. The cages rested on plastic pots filled with water. A cotton roll (diameter 5 mm, length 40 mm) was inserted through a hole centered in the bottom of each cage. By protruding from the bottom of the cage into the pot of water, the cotton roll remained water logged for the duration of each test and provided humidity and drinking water for the spiders and the ants inside the cage. Four green mango leaves (each *c.* 150 mm long), each still attached to a stem (one leaf per stem, stem *c.* 200 mm long), were wedged into each cage. Numerous trials were run simultaneously.

A large number of major workers were collected from a single representative colony of *O. smaragdina* in a mango tree. These ants were then maintained as a 'laboratory colony' in a large terrarium. From this large laboratory colony, we established smaller groups in the cages by placing a specified number (10, 20, 40) of workers in each cage 16 h before testing began. Whenever the laboratory colony was depleted, we replenished it by collecting

more major workers from the same field colony as before.

Testing began by introducing a single salticid through one of the cork holes at the top of the cage, with a rule that no ants could be within 50 mm of the hole when the salticid was introduced. With four cork holes to choose from, this criterion was always achievable. Each test spider was first taken into a 40 mm long (diameter 5 mm) clear glass tube (plugged by a cork at both ends). After 10 min the corks from the tube and a hole in the top of the cage were removed and the open end of the tube was placed against the open hole of the cage. If the spider did not enter the cage immediately, the cork at the other end of the tube was removed and a brush was used gently to push the spider out of the tube and into the cage. For each combination of salticid species and each ant-group size, equal numbers of tests ($n = 100$) were carried out. Between tests, cages were wiped clean with 80% ethanol, followed by distilled water. Transfer tubes and corks were also cleaned with 80% ethanol, followed by distilled water. The cleaning routine was a precaution against the possibility that chemical traces from previous ants and salticids might influence test outcomes.

RESULTS

Data from testing with each ant-group size are considered separately. However, within each group size, we pooled many of the data sets that were not significantly different from each other (in each instance, $P > 0.1$). For each species of salticid data for adults were pooled with data for juveniles. Data for the various species within each category were also pooled, resulting in three sets of pooled data (myrmecophagic, myrmecomorphic and ordinary). Data for myrmecophagic, myrmecomorphic and myrmecophilic salticids were then pooled and compared with *Myrmarachne assimilis* and with ordinary salticids, greatly simplifying data presentation. However, the trends from using myrmecophagic, myrmecomorphic and myrmecophilic salticids also held, and were statistically significant, when myrmecophagic and myrmecomorphic salticids were each compared alone with *M. assimilis* and with ordinary salticids.

With each of the three ant-group sizes, the % survival of ordinary salticids was significantly less than that of myrmecophagic, myrmecomorphic and myrmecophilic salticids (pooled) ($X^2 = 974.57$, $P < 0.001$, 10 ant tests) ($X^2 = 855.89$, $P < 0.001$, 20 ant tests) ($X^2 = 80.95$, $P < 0.001$, 40 ant tests) (Fig. 1). With groups of 40 ants, the % survival of *M. assimilis* was not significantly different from that of myrmecophagic, myrmecomorphic and myrmecophilic salticids (pooled) ($X^2 = 3.17$, $P = 0.075$). However, with smaller ant groups (20 or 10), the survival rate of *M. assimilis* was significantly higher than that of myrmecophagic, myrmecomorphic and myrmecophilic salticids (pooled) ($X^2 = 19.49$, $P < 0.001$, 10 ant tests) ($X^2 = 23.84$, $P < 0.001$, 20 ant tests).

DISCUSSION

The vicinity of weaver-ant colonies appears to be particularly dangerous for salticids, including salticids that mimic ants (i.e., ants are 'enemies'). In groups of 40 ants, few salticids survived, regardless of category. In groups of 10 and 20 ants, salticid survival fell into three clusters. Ordinary salticids had the lowest proportion of survivors and *M. assimilis* had the highest. Myrmecomorphic salticids (other than *M. assimilis*), myrmecophagic salticids and the myrmecophilic species (*Phintella piatensis*) had intermediate survival values.

That ordinary salticids had the lowest percentage of survivors was consistent with the earlier study (Nelson et al. 2004), but there were also some differences between the findings in this study and the earlier study. In the earlier study, ant mimics, ant eaters and *P. piatensis* (the myrmecophile) had distinguishably different survival values, but these categories were not discernible in the present study where we used groups of 10–40 ants. Another difference was that, in the earlier study, the proportion of surviving *M. assimilis* did not differ significantly from that of other ant mimics with a variety of ant species, whereas *M. assimilis* was clearly distinguishable from other ant mimics in the present study using only *O. smaragdina*.

For any salticid, avoidance might be the most straightforward protection from attacks by ants. Although spider eyes generally lack the structural complexity required for acute vision (Land 1985), salticids have unique, complex eyes (Land 1969a,b; Blest et al. 1990) that support resolution abilities with no

Figure 1.—Percent survival of different categories of salticids in tests with groups of *Oecophylla smaragdina* (Table 1). For each salticid species, with each ant-group size, $n = 200$ (100 adults and 100 juveniles). Data pooled in histograms. n for pooled data is indicated above each bar.

known parallels in other animals of comparable size (Land & Fernald 1992; Land & Nilsson 2002). Exceptional eyesight may enable salticids to be especially effective at detecting ants from a distance and avoiding dangerous proximity, but the strategies of myrmecophilic, myrmecomorphic and myrmecophagic salticids cannot be simply to avoid ants. For example, myrmecophagic salticids must at least intermittently come close enough to attack individual ants.

For *Myrmarachne*, the resemblance to the ant model appears to function primarily as Batesian mimicry. *Myrmarachne*'s mimicry of an aggressive model puts these salticids in a difficult situation. Successfully using mimicry to achieve safety from other predators would seem to require that individuals of *Myrmarachne* come close to the ants that serve as their models, but they must, at the same time, avoid becoming the model's prey (see Reiskind 1970; Edmunds 1974; Elgar 1993; Oliveira 1988). For *M. assimilis*, the problem is specifically how to stay close enough to be an effective Batesian mimic of one of its own especially dangerous predators, *O. smaragdina* (Nelson et al. 2004).

Our hypothesis was that *M. assimilis* has evolved adaptations that make it especially proficient at surviving in the presence of its model and our findings support this hypothesis. However, further research is needed for clarifying precisely what these adaptations might be. Ants rely primarily on chemical, not visual, information for detecting other ants (Hölldobler & Wilson 1990). Many ants use cuticular hydrocarbons to distinguish between nestmates and non-nestmates (Hölldobler & Wilson 1990; Thomas et al. 1999; Wagner et al. 2000). The salticid spider *Cosmophasis bitaeniata* (Keyserling 1882) associates with *O. smaragdina* and is an exploitative chemical mimic of its host (Allan & Elgar 2001; Allan et al. 2002). Whether *M. assimilis* uses a similar strategy to avoid predation by *O. smaragdina* while in the vicinity of its model has not been investigated. However, in this study, the salticids were from laboratory cultures and, unless it was during the duration of the tests itself, they could not have acquired any host-specific cuticular hydrocarbons from ants by direct contact with, or close proximity to, the ants.

ACKNOWLEDGMENTS

Work in the Philippines was generously assisted by the International Rice Research In-

stitute (IRRI). We are especially grateful to Kong Luen Heong and Tom W. Mew for the numerous ways in which they supported the research and to the following IRRI staff for technical assistance: Elpie Hernández, Errol Rico, Glicerio Javier, Josie Lynn Catindig and Clod Lapis. This research was funded in part by a grant to R.R.J. from the Marsden Fund of the New Zealand Royal Society (UOC512).

LITERATURE CITED

Allan, R.A. & M.A. Elgar. 2001. Exploitation of the green tree ant, *Oecophylla smaragdina*, by the salticid spider *Cosmophasis bitaeniata*. Australian Journal of Zoology 49:129–137.

Allan, R.A., R.J. Capon, W.V. Brown & M.A. Elgar. 2002. Mimicry of host cuticular hydrocarbons by salticid spider *Cosmophasis bitaeniata* that preys on larvae of tree ants *Oecophylla smaragdina*. Journal of Chemical Ecology 28:835–848.

Blest, A.D., D.C. O'Carroll & M. Carter. 1990. Comparative ultrastructure of Layer I receptor mosaics in principal eyes of jumping spiders: the evolution of regular arrays of light guides. Cell and Tissue Research 262:445–460.

Cushing, P.E. 1997. Myrmecomorphy and myrmecophily in spiders: a review. Florida Entomologist 80:165–193.

Doflein, F. 1905. Beobachtungen an den Weberameisen (*Oecophylla smargdina*) Biologisches Cenrablatt 25:497–507.

Edmunds, M. 1974. Defence in Animals. London, Longman.

Edmunds, M.E. 2000. Why are there good and poor mimics? Biological Journal of the Linnean Society 70:459–466.

Elgar, M.A. 1993. Inter-specific association involving spiders: kleptoparasitism, mimicry and mutualism. Memoires of the Queensland Museum 33:411–430.

Elgar, M.A. & R.A. Allan. 2004. Predatory spider mimics acquire colony-specific cuticular hydrocarbons from their ant model prey. Naturwissenschaften 91:143–147.

Hölldobler, B. 1983. Territorial behavior in the green tree ant (*Oecophylla smaragdina*). Biotropica 15:241–250.

Hölldobler, B. & E.O. Wilson. 1977a. Weaver ants. Scientific American 237:146–154.

Hölldobler, B. & E.O. Wilson. 1977b. Weaver ants: social establishment and maintenance of territory. Science 195:900–902.

Hölldobler, B. & E.O. Wilson. 1977c. Colony-specific territorial pheromone in the African weaver ant *Oecophylla longinoda* (Latreille). Proceedings of the National Academy of Sciences of the United States of America 74:2072–2075.

Hölldobler, B. & E.O. Wilson. 1978. The multiple recruitment systems of the African weaver ant *Oecophylla longinoda* (Lareille) (Hymenoptera: Formicidae). Behavioral Ecology and Sociobiology 3:19–60.

Hölldobler, B. & E.O. Wilson. 1990. The Ants. Heidelberg, Springer-Verlag.

Jackson, R.R. & S.E.A. Hallas. 1986. Comparative biology of *Portia africana*, *P. albimana*, *P. fimbriata*, *P. labiata*, and *P. schultzi*, araneophagic web-building jumping spiders (Araneae: Salticidae): utilization of silk, predatory versatility, and intraspecific interactions. New Zealand Journal of Zoology 13:423–489.

Jackson, R.R. & S.D. Pollard. 1996. Predatory behavior of jumping spiders. Annual Review of Entomology 41:287–308.

Jackson, R.R. & M.B. Willey. 1994. The comparative study of the predatory behaviour of *Myrmarachne*, ant-like jumping spiders (Araneae, Salticidae). Zoological Journal of the Linnean Society 110:77–102.

Land, M.F. 1969a. Structure of the retinae of the eyes of jumping spiders (Salticidae: Dendryphantinae) in relation to visual optics. Journal of Experimental Biology 51:443–470.

Land, M.F. 1969b. Movements of the retinae of jumping spiders (Salticidae: Dendryphantinae) in response to visual stimuli. Journal of Experimental Biology 51:471–493.

Land, M.F. 1985. The morphology and optics of spider eyes. Pp. 53–78. *In* Neurobiology of arachnids (Barth, F. G. ed). Springer-Verlag, Berlin.

Land, M.F. & R.D. Fernald. 1992. The evolution of eyes. Annual Review of Neuroscience 15:1–29.

Land, M.F. & D.E. Nilsson. 2002. Animal Eyes. Oxford, Oxford University Press.

Li, D. & R.R. Jackson. 1996. Prey-specific capture behaviour and prey preferences of myrmecophagic and araneophagic jumping spiders (Araneae: Salticidae). Revue Suisse de Zoologie hors Serie 423–436.

Lokkers, C. 1986. The distribution of the weaver ant, *Oecophylla smaragdina* (Fabricius) (Hymenoptera: Formicidae) in Northern Australia. Australian Journal of Zoology 34:683–687.

Nelson, X.J., R.R. Jackson, S.D. Pollard, G.B. Edwards & A.T. Barrion. 2004. Predation by ants on jumping spiders (Araneae: Salticidae) in the Philippines. New Zealand Journal of Zoology 31: 45–56.

Oliveira, P.S. 1988. Ant-mimicry in some Brazilian salticid and clubionid spiders (Araneae: Salticidae, Clubionidae). Biological Journal of the Linnean Society 33:1–15.

Reiskind, J. 1970. Multiple mimetic forms in an ant-mimicking clubionid spider. Science 169: 587–588.

Rice, W.R. 1989. Analysing tables of statistical tests. Evolution 43:223–225.

Sokal, R.R. & F.J. Rohlf. 1995. Biometry: the Principals of Statistics in Biological Research. 3rd ed. New York, W. H. Freeman & Co.

Thomas, M.L., L.J. Parry, R.A. Allan & M.A. Elgar. 1999. Geographic affinity, cuticular hydrocarbons and colony recognition in the Australian meat ant *Iridomyrmex purpureus*. Naturwissenschaften 86:87–92.

Vanderplank, F.S. 1960. The bionomics and ecology of the red tree ant *Oecophylla* sp. and its relationship to the coconut bug *Pseudotheraptus wayi* Brown (Coreidae). Journal of Animal Ecology 29:15–33.

Wagner, D., M. Tissot, W. Cuevas & D.M. Gordon. 2000. Harvester ants utilize cuticular hydrocarbons in nestmate recognition. Journal of Chemical Ecology 26:2245–2257.

Wanless, F.R. 1978. A revision of the genera *Belippo* and *Myrmarachne* (Araneae: Salticidae) in the Ethiopian region. Bulletin of the British Museum of Natural History 33:1–139.

Manuscript received 11 February 2004, revised 27 September 2004.

2005. The Journal of Arachnology 33:820–825

A NEW TECHNIQUE FOR EXAMINING SURFACE MORPHOSCULPTURE OF SCORPIONS

Erich S. Volschenk[1]: Curtin University of Technology, School of Environmental Biology, GPO Box U 1987, Perth, Western Australia 6845, Australia; Western Australian Museum, Francis Street, Perth 6000, Western Australia, Australia; and Queensland Museum, Box 3300, South Brisbane, Queensland, 4101, Australia.

ABSTRACT. A new technique for examining the exomorphology of the scorpion epicuticle is described that utilizes the fluorescent property of scorpion cuticle. Fluorescence of the scorpion exoskeleton under longwave ultraviolet light is a well known property previously only utilized for the capture or observation of scorpions at night. Fluorescence is an energy emission that is analogous to the secondary electron emissions utilized in electron microscopy to provide information about surface detail. This new technique is fast, inexpensive and non-destructive, and provides an alternative means of documenting of surface macrosculpture for the description and identification of scorpion species.

Keywords: Fluorescence, scorpion, epicuticle, exomorphology, images

Among the many unique and unusual features that scorpions exhibit, arguably the most curious is their fluorescence on exposure to long wavelength UV (ultraviolet light). Fluorescence is an energy (light) emission that results from the excitation of electrons in certain compounds by light of specific wavelengths. Once excited by a photon, the electrons of these compounds almost immediately return to their previous energy state, and simultaneously a lower level energy emission (visible light) results.

Pavan (1954a) first demonstrated that UV light of wavelength 366.3 nm causes maximum fluorescence of scorpion epicuticle. Scorpion fluorescence has captivated the interest of researchers (Honetschlacher 1965; Lawrence 1954; Williams 1980) since it was revealed that they exhibit this curious phenomenon. Pavan (1954a, 1954b) found that the fluorescence emanates from the outermost layer of the cuticle, the epicuticle, but was unable to discover the fluorescent compound or compounds. More recently, Stachel and Stockwell (1999) isolated the fluorescent compound, β-carboline, from scorpion epicuticle. The intensity of scorpion fluorescence varies among species and the time elapsed since the last molt, and non-fluorescent scorpions are unknown (Stahnke 1972). Despite a reasonable understanding of the origins of the fluorescence in scorpions, there is still no consensus as to why this phenomenon exists. The fluorescent property has to date been exploited most successfully as a tool in their observation, detection or capture (Stahnke 1972). Scorpions are predominantly nocturnal and, equipped with a blacklight, a researcher can find many more specimens, as well as species, at night than is possible during the day with an equivalent searching effort (Honetschlacher 1965; Lamoral 1979; Sissom et al. 1990; Williams 1980).

Images of biological specimens made from SEM (scanning electron microscopes) predominantly utilize the detection of emission of SEs (secondary electrons) to form digital images. Secondary electrons result when a focused beam of electrons of sufficient acceleration voltage passes over a suitable (conductive) subject, typically of high molecular mass. High energy electrons from the primary beam displace loosely bound outer-orbital electrons in the subject, and SEs are emitted from the surface of the specimen. These SEs have a different voltage (energy) to that of the electron beam that scans the surface of the

[1] Corresponding address: Department of Invertebrate Zoology, American Museum of Natural History, 79th street @ Central Park West, New York, NY. 10024, United States of America. E-mail: evolsche@amnh.org

Figure 1.—Carapace of *Lychas* sp.1. from Australia (WAM; conventional image (scale bar = 1mm).

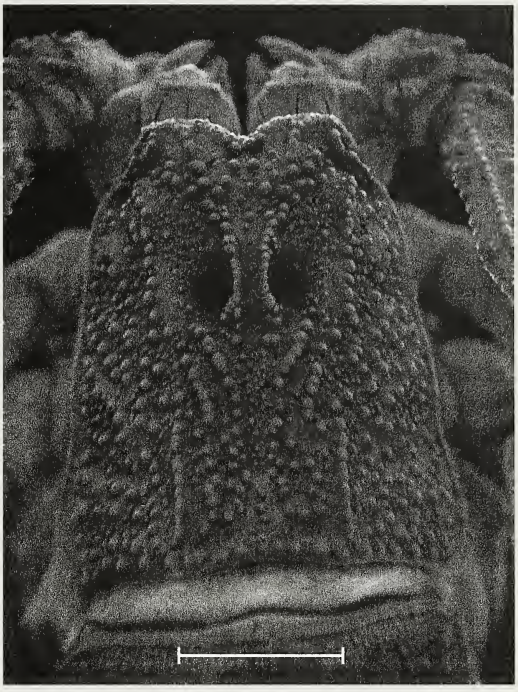


Figure 2.—Carapace of *Lychas* sp.1. from Australia, fluorescence image (scale bar = 1mm).

specimen and are principally utilized in the production of images of surface detail from electron microscopes. The production of the SE emission in an electron microscope is analogous to the light emission called fluorescence, and prompted the author to considered experimentation with imaging of cuticular surface detail from the fluorescence of scorpions. The surface sculpturing (granulations and carinae) of scorpions is frequently utilized in the identification of species (Lamoral 1979; Sissom 1990), however, this useful character can be difficult to examine as it is often obscured by complex color patterns lying beneath the cuticle. Images made using this fluorescence technique were recently published by Prendini (2003a, 2003b, 2003c) and further exemplify its usefulness.

METHODS

The specimens used to exemplify this technique are lodged in the Western Australian Museum: *Lychas* sp. 1 (ESV2255), *Lychas* sp.2 (T56392) and *Lychas variatus* (Thorell 1876) (WAM 97/1226); and the Queensland Museum: *Hemilychas alexandrinus* (Hirst 1911) (S58519). Images were taken with a Leica DC100 digital camera attached to a Leica MZ6 stereo dissection microscope, fitted with an iris diaphragm. Standard illumination was provided from a Leica light source. Ultraviolet illumination was provided from modified portable blacklight units normally utilized in the field detection and collection of scorpions. Each unit consisted of a portable 12V fluorescent light fixture, fitted with two black light tubes (National, FL8 BL-B), and powered by a 12V rechargeable lead-acid battery (Panasonic, LC-R127R2P). When fluorescence images were being taken, the two blacklights were placed on either side of the specimen. Specimens were imaged at night to minimize extraneous light. Conventional illumination was used, with the iris diaphragm fully constricted to provide maximum depth of field, to position and focus the image, after which the blacklights were switched on and all other sources of illumination (except computer monitor which was turned away from the microscope) were switched off. All images were taken with the slow imaging option of the DC100 software, owing to the lower intensity of the fluorescence, longer periods (up

Figure 3.—Mesosomal tergites of *Lychas* sp.2. from Australia, conventional image (scale bar = 1mm).

Figure 4.—Mesosomal tergites of *Lychas* sp.2. from Australian, fluorescence image (scale bar = 1mm).

to 10 seconds) were required per image capture.

For imaging, each specimen was placed into a small glass petri dish with enough 90–100% ethanol to just cover it. The clarity of the image deteriorated considerably as the depth of ethanol above the specimen increased. More dilute concentrations of ethanol were also trialed, however 70–80% mixtures developed a faint scum over the surface that decreased the clarity of the images.

Images of epicuticle fluorescence were in shades of blue, and these were converted to greyscale in the graphics editing package Corel™ Photo-Paint (version 7). Some images were also enhanced for publication by making minor improvements to levels of brightness and contrast, the same adjustments typically being conducted on images made using a SEM. The technique described in this contribution is exemplified using four different species of Australian buthids.

RESULTS

Fluorescence images (Figs. 2, 4, 6 & 8) reveal grey scale surface detail and structure of the external sculpturing of scorpion exoskeleton. Conventional imaging under ethanol almost completely obscures the surface sculpturing in images, (Figs. 1, 3, 5 & 7) but provides accurate documentation of color patterning. Surface detail revealed in the fluorescent images mimics those obtained from scanning electron microscopes except that setae and macrosetae are not revealed, and the depth of field is relatively shallow.

Figures 1 and 2 depict the carapace of *Lychas* sp. 1, an undescribed species from Australia. The specimen had become badly distorted during or following preservation (tissue displacement was evident beneath the cuticle). Consequently, under conventional illumination the carapace had a glassy semitransparent appearance, resulting from light reflecting from beneath the carapace. The fluorescent image reveals only the surface detail and this detail could accurately be compared with more intact specimens or similarly damaged specimens to facilitate the identification of more intact specimens of this species. Figures 3 and 4 depict the mesosomal tergites of *Lychas* sp. 2, another undescribed *Lychas* species from Australia. Figure 5 depicts the ornately patterned carapace of *Lychas variatus*

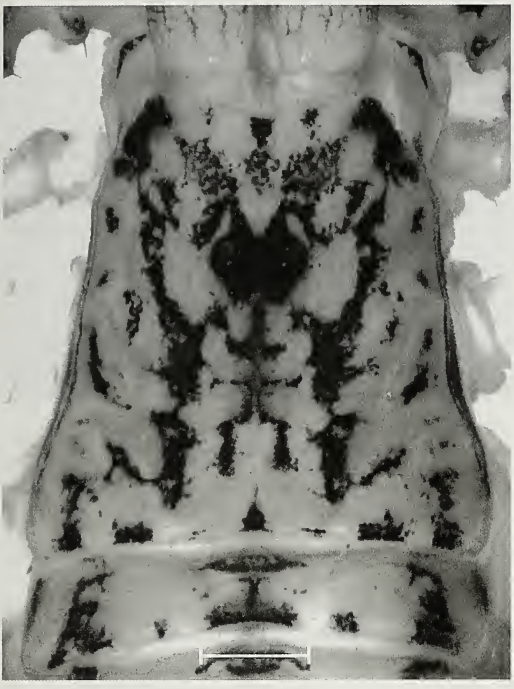


Figure 5.—Carapace of *Lychas variatus* (Thorell 1876), conventional image (scale bar = 1mm).

Figure 6.—Carapace of *L. variatus*, fluorescence image (scale bar = 1mm).

while the fluorescent image (Fig. 6) reveals the poorly sculptured surface. Figures 7 and 8 depict the lateral aspects of metasomal segment V of *Hemilychas alexandrine*, another Australian buthid. The finely reticulate pattern is seen in Fig. 7 using standard illumination, whereas punctated nature of this metasomal segment is revealed in the fluorescent image, Fig 8. In this case the fluorescent image revealed surface detail not associated with granulations, but with punctations.

DISCUSSION

The technique described here, for imaging scorpions under UV light provides images with detail similar to those taken with a scanning electron microscope. Unlike specimens examined in a conventional SEM, those from which the fluorescence images were made were not coated in conductive material and were taken under normal atmospheric conditions. Fluorescence imaging is a non-destructive technique that can be applied to type specimens. These images reveal information about the surface sculpturing of the cuticle that may otherwise be obscured or over-enhanced by subcuticular pigmentation. Images of scorpion fluorescence are proposed to augment line drawings for the documentation of surface sculpture in scorpions. This imaging protocol provides a much cheaper substitute for SEM. Using a digital camera, mounted to a dissection microscope, images can be taken as quickly or slowly as possible and adjustment of the specimen can be made directly and immediately. A particular advantage of this technique over SEM is the ability to manage very large specimens. Many scorpions are too large to be examined examined using SEM without dissecting the specimen before mounting the area of interest onto a stub. The fluorescent technique described here can be applied to large scorpions without dissecting the specimen.

Some drawbacks of this technique relate to the low depth of field experienced at high magnifications, and a slightly grainy appearance to the images. The relatively large size of scorpions, compared with most other chelicerates, implies that low depth of field issues are not likely to be experienced unless imaging the smallest of scorpions, or very small structures such as chelicerae and tarsi. An ad-

Figure 7.—Lateral aspect of metasoma V of *Hemilychas alexandrinus* (Hirst 1911), conventional image showing color patterning and some setation (scale bar = 1mm).

Figure 8.—Lateral aspect of metasoma V of *H. alexandrinus*: fluorescence image, showing surface punctations (scale bar = 1mm).

ditional drawback is the non-fluorescent nature of setae and macrosetae, making this technique unsuitable for investigation into chaetotaxy. Interestingly, the base of some setae and the areoles of trichobothria typically fluoresce more brightly than the surrounding surfaces and this property can assist in the location of trichobothria. The quality of digital images has improved considerably since this study was conducted, and smoother images are already characteristic of high resolution digital cameras. With the application of fluorescent stains and histological preparations, this technique may be applicable to other organisms that do not naturally fluoresce.

ACKNOWLEDGMENTS

This paper formed part of the author's doctoral thesis, which was supported by a Curtin University Postgraduate Scholarship, and research grant from ABRS (Australian Biological Resources Study). I thank Prof. Jonathan Majer (Curtin University of Technology) for the use of his digital camera and microscope set-up. Thanks are also given to Dr. Mark Harvey and Dr. Bill Humphreys (Western Australian Museum), Dr. Robert Raven (Queensland Museum), Dr. Lorenzo Prendini (American Museum of Natural History) and Dr. David Sissom (West Texas A&M University) and the two anonymous referees who provided constructive reviews of earlier versions of this paper.

LITERATURE CITED

Hirst, S. 1911. Descriptions of new scorpions. Annals and Magazine of Natural History (8) 8:462–473.

Honetschlacher, L.D. 1965. A new method for hunting scorpions. Turtox News 43:69–70.

Lamoral, B.H. 1979. The Scorpions of Namibia (Arachnida: Scorpionida). Annals of the Natal Museum 23:497–784.

Lawrence, R.F. 1954. Fluorescence in Arthropoda. Journal of the Entomological Society of Southern Africa 17:167–170.

Pavan, M. 1954a. Primi dati per la caraterizzazione della sostanza fluorescente nel tegumento degli scorpioni. Bolletino Societa Italiana Biologia Sperimentale 30:803–805.

Pavan, M. 1954b. Studi sugli scorpioni I, una nuova caratteristica tipica del tegumentodegli scorpioni. Italian Journal of Zoology 21:283–291.

Prendini, L. 2003a. Discovery of the male of *Parabuthus muelleri*, and implications for the phylogeny of *Parabuthus* (Scorpiones: Buthidae). American Museum Novitates 3408:1–24.

Prendini, L. 2003b. A new genus and species of bothriurid scorpion from the Brandberg Massif, Namibia, with a reanalysis of bothriurid phylogeny and a discussion of the phylogenetic position of *Lisposoma* Lawrence. Systematic Entomology 28:149–172.

Prendini, L. 2003c. Systematics and biogeography of the family Scorpionidae (Chelicerata: Scorpiones), with a discussion on phylogenetic methods. Invertebrate Systematics 17:185–259.

Sissom, W.D. 1990. Systematics, biogeography, and paleontology. *In* G. A. Polis (ed) Systematics, biogeography, and paleontology. Stanford University Press, Stanford, pp. 64–160.

Sissom, W.D., G.A. Polis and D.D. Watt. 1990. Field and Laboratory methods. *In* G. A. Polis (ed) Field and Laboratory methods. Stanford University Press, Stanford, pp. 445–461.

Stachel, S.L., S.A. Stockwell and D.L.V. Vranken. 1999. The fluorescence of scorpions and cataractogenesis. Chemistry and Biology 6:531–539.

Stahnke, H.L. 1972. UV light, a useful field tool. Bioscience 22:604–607.

Thorell, T. 1876. Etudes scorpiologiques. Atti Societe Italienne de Sciences Naturelles 19:75–272.

Williams, S.C. 1980. Scorpions of Baja California, Mexico, and adjacent islands. Occasional Papers of the California Academy of Sciences 135:1–127.

Manuscript received 9 July 2003, revised 30 June 2004.

2005. The Journal of Arachnology 33:826–849

THE EMERGENCE OF MANIPULATIVE EXPERIMENTS IN ECOLOGICAL SPIDER RESEARCH (1684–1973)

James R. Bell: Warwick HRI, Wellesbourne, Warwickshire. CV35 9EF. UK. E-mail: j.r.bell@warwick.ac.uk

ABSTRACT. The history of spider ecology is discussed from its early beginnings in 1684 when the natural historian Martin Lister published his observations, to the post-war period up until 1973 when ecological spider research gathered momentum. While there have been many important observations since Lister, spider ecology appeared explicitly in the titles of papers only after the turn of the 20th century. However, much of what was published up until the 1950s is of little scientific value because these works contained natural history notes and conjecture, not manipulative experimentation. The exception was a paper written in 1939 by Pontus Palmgren who was not an ecologist but paradoxically a functional anatomist with a particular interest in ornithology. His paper was in the spirit of Ernst Haeckel's original definition of ecology that was seen as synonymous with physiology, a legacy that was detected in many of the papers decades after Palmgren. However, there was little evidence that ecological theory was being tested. Instead, theoretical inputs were largely ignored with most spider ecologists preferring to pursue the somewhat circular interest of basic observational studies. Eventually after some considerable delay, Charles Elton's theories of the niche and succession fed into spider ecology but the papers were often weak and invariably flawed due to the absence of experimental manipulations. Notably, it was not until the 1950s, when the elegant experiments of Edwin Nørgaard who manipulated the system in order to understand the interactions between spiders and their environment, that scientific spider ecology began. Edwin Nørgaard should be credited as the father of 'spider ecology', although Matthias Schaefer and Sven Almquist also made important contributions to the field and should not be overlooked. These researchers employed manipulative techniques during a period in which this experimental approach was not widely used in spider ecology. I conclude this review with a look to the future and predict that model selection will become much more prevalent, although it will never replace manipulative experimentation. One outstanding issue that has remained since 1684 has been the gift of ecological theory to the wider scientific community. Although spider ecologists have received theoretical frameworks from other disciplines such as botany and entomology, they have never reciprocated although they are now well placed to do so.

Keywords: Ecology, Nørgaard, inductive method, history of science

In this review, the aim is to trace the early advances in spider ecology to individual authors who were instrumental in shaping our current understanding of ecology as a modern science. The motivation for this paper is to reveal to the ecological community some of the best early research in the first half of the 20th century when it is believed that ecological spider experiments really began. This period has remained elusive to most researchers, because the majority of ecological literature pre-1970 is not available electronically and ecological research tends to have a short citation life-time which rarely extends beyond a decade. For example, there are two excellent, but very similar experiments on orientation in *Frontinella communis* (Hentz 1850) (Linyphiidae). The first by Pointing (1965) was not picked up by Suter (1981) or those who did the peer review and editing, simply because the reference was not in general electronic circulation (Robert Suter pers. comm.). This is not especially embarrassing because for most authors there has rarely been a need to look deep into the scientific literature—in fact, ecological journals positively discourage it.

Contrast this experience in ecology with that of spider taxonomy in which investigators can turn to a series of catalogues that list nearly all the publications since Clerck in 1757 (e.g., Platnick 2005). Taxonomists have the expectation that all important texts will be cited independent of date of original publication, even if a paper is drawn from the eighteenth century. Ecology would sometimes do well to embrace the citation ethos that taxonomy is unique in upholding. There is a strong argument to suggest that ecology may have come

out of the doldrums much more quickly if studies were read, cited and then developed further. Instead, it seems that many of the individuals working during the embryonic phase in spider ecology, studied in isolation with few, if any, academic exchanges.

Ecology could be described as a new science because it is less than 150 years old and, for example, only one tenth the age of "Aristotelian" taxonomy. Its formal beginnings were in 1866 when this new branch of science was erected by Ernst Haeckel, a German invertebrate zoologist. Haeckel coined the word "ecology" in his book "Generelle Morphologie der Organismen" from the Greek, "oikos" meaning the study of the home. Ecology has always been defined quite loosely, but in this review it is defined as the scientific study of the abiotic (e.g., temperature) and biotic (e.g., competition) interactions between organisms and their natural environment. Implicitly, ecology contains a field component and is not purely laboratory based.

Defining ecological spider research as scientific.—There is a need to make objective judgments about which papers have scientific merit, versus those that have no scientific merit. To assess papers for scientific merit, there is a need to be clear about what parameters underpin science. Although there is general agreement that the first scientist was the 6th century B.C. Greek Thales of Miletus, the scientific method with which we are familiar today evolved during a revolution of thinking during the 16th century onwards. Ecologists generally follow the scientific protocol known as the inductive method, rather than the classical deductive method practiced by a handful of Bayesian ecologists and the great majority of physicists (Popper 1977; Murray 2001; Oksanen 2001). This distinction is important because ecologists are often not aware of the dichotomy between these approaches or the implications of applying either approach to their research. The replicated, randomized designs typical of the inductive methods are a vital tool to ecologists who will find the pervasive use of universal laws an anathema—the reverse is true for a deductivist. Oksanen (2001) criticizes such a clear distinction arguing for the hybrid approach in which ecologists switch scientific philosophies depending on the scale of the system and the constraints on replication and randomization. In the current climate, he has mild (Cottenie & De Meester 2003) or no support (Hurlbert 1984, 2004), but it will be interesting to see how, or indeed if, this debate will change the way ecological experiments are done in the future. Unlike physics, nearly all ecologists will argue that "laws" are absent from ecology because organisms cannot so easily be pigeon-holed. Consider the statement that "all spiders are entirely carnivorous in the presence of a diversity of prey." This was the perceived view until very recently when it was found that a small minority of spiders intentionally supplement their diet with nectar and pollen (Jackson et al. 2001; Ludy 2004). That is not to say that all of ecology is without basic rules, since theorems are often used and are sometimes law-like in nature (Turchin 2001).

Not all ecologists are theory driven, but all recognize that ecology is empirical and therefore implicitly include at least one experiment. It is strongly argued by many that experimental ecology should include a hypothesis to formalize the procedure (Wise 1993 and see Ricklefs & Miller 1999 for approach). The approach to formalizing a hypothesis is poorly defined, not least because there are multiple opinions of what constitutes a hypothesis (Platt 1964; Connor & Simberloff 1986). In the context of this paper, I simply refer to hypotheses as questions or statements that are to be tested, accepting that this definition is not all-encompassing. Classically, hypotheses were of the null form (i.e., statement of no relationship; a negative statement), which have been heavily criticized in ecology and are now not widely used (Quinn & Dunham 1983; Turchin 1999; Anderson et al. 2000; Murray 2001). Instead, science now encompasses many variants including statistical (i.e., the use of predictors and probabilities to evaluate relationships) and alternative hypotheses (i.e., statement of a relationship; a positive statement), all of which I consider valid for the purpose of this review (Platt 1964; Johnson 1999; Anderson et al. 2000).

Ecological research that has gained the most credibility has been that which includes manipulative experiments to control more clearly the effects of a variable on a subject (Hairston 1989; Wise 1993; Ricklefs & Miller 1999; Hurlbert 2004). Without manipulation, ecology becomes very generalized and has

very little explanatory power because it lacks the appropriate conditions and controls. Such studies that are without manipulation can only be suggestive, rather than explicit tests of hypotheses and tend to be observational. Observational studies occupy a "half-way house" between natural history and formal science (Lubchenco & Real 1991; Wise 1993). Observational studies have an empirical basis, but no treatment structure and represent much of what spider ecologists practice. While this method is not a test of a hypothesis, it forms the essential groundwork for later explicit testing and is a valuable scientific tool as long as the results are not overstated.

There is a need to make a distinction between ecology and other related disciplines. Natural history and faunistics often purport to be a branch of ecology and are sometimes referred to as "scientific." Without exception these neither present any kind of hypothesis or manipulation and are without any rigid experimental framework. Further evolved is theoretical ecology which replaces the field component with mathematical simulation. Common to these three disciplines are that they can only generate new hypotheses and concepts, but they can never be a real test of them. Consequently, theoretical ecology, natural history and faunistics will not be at the center of this review, but are implicit in the evolution of ecology as a discipline and will be referred to throughout.

METHODS

Literature search.—In the trawl of ecological publications for this review, all empirical experiments up to 1973 have been considered. The process of deciphering whether hypotheses were apparent in a paper has been at times, extremely difficult and on other occasions quite straight forward. This is because some authors were quite explicit about their intentions expressing them in bullet form (e.g., Hypothesis 1, 2 and 3 etc.), while others were much more discrete. I have tried to highlight both cases, but will have inevitably failed to classify all types correctly. Thus, I offer my interpretations of what hypotheses are being tested as suggestive, but not conclusive. What was easier to assess was the quality of the empirical data as well as the subject or its environment being tested. In the review, I have drawn attention to some of the best manipulations and highlighted others that I have felt to be fundamentally erroneous. Until the 1950s, results were rarely rationalized through the use of any statistics, therefore I have not imposed the need for statistical tests so long as data have been given appropriate interpretation. Thus, the best examples I highlight follow a logical sequence of hypothesis statements, experimental manipulation, data acquisition and rationalization, which I identify as the benchmark for the purposes of this review.

For the review of the spider literature, Pierre Bonnet's "Bibliographia Araneorum" (Bonnet 1945) which lists 8000+ papers from Aristotle to 1939 was used—all titles were read in combination with the online database JSTOR which covered the period 1684–1973. Post 1939, the Zoological Record replaced Bibliographia Araneorum. For both Bonnet and the Zoological Record, the search term "ecolog*" and its linguistic derivatives "ökolog*/ecologisch*/ekologitsch*" were selected as keywords that might appear in the title of an ecological paper. For the JSTOR search (1684–1973), all papers that included one or more of the following keywords "spider, spiders, ecology, ecological, aranea, araneae" were read. Additionally, the "Web of Science" online database was searched using the terms "aranea* OR spider* NOT mite* NOT monkey*" from 1970, the date of its inception, to 1973. While these keyword searches are not a "catch-all" of the entire ecological literature, it does strike at the center of the subject. Once papers were identified, they were critically examined for evidence of a hypothesis, experimental framework, manipulation etc, as described above. The limitation of this study is that papers published in non-European languages have not been analyzed.

THE HISTORY OF ECOLOGICAL SPIDER RESEARCH

The ecological spider literature between 1684 and 1956: a period of slow development.—The illusion that readers may have is that ecology started early in the 19th century, as a literature scan reveals a plentiful supply of "ecological" publications. For example, a paper by Boys (1880) on the influence of the tuning fork on the orb web of the garden spider appears to be a promising ecological investigation, detailing how he simulated the vi-

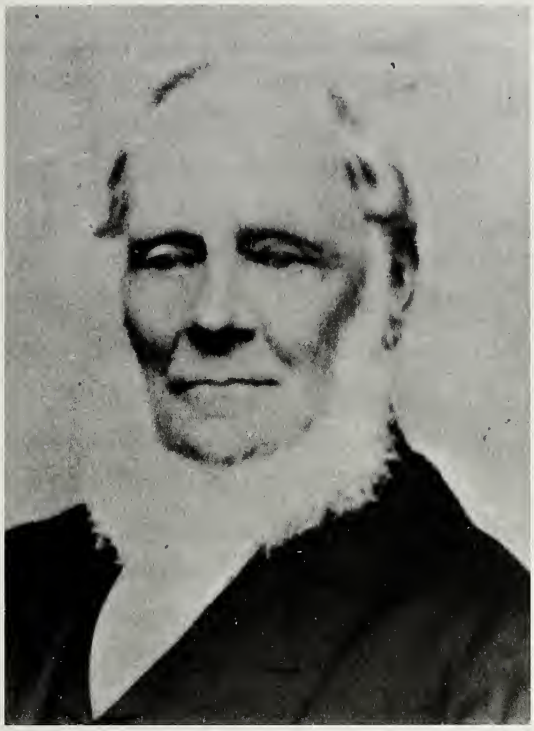


Figure 1.—John Blackwall (1790–1881) is credited as the first to recognize the taxonomic importance of the male palpus. Other than his taxonomic work, he also conducted behavioral experiments on spiders, including those on ballooning motivation, in which he referred to hypotheses. Additionally, he also wrote 15 papers on ornithology and is recognized as having made an important contribution to the study of bird migration. Source: Photo Bonnet (1945) plate IV. Note: The Natural History Museum, London holds many portraits of scientists, but the original of John Blackwall appears to have been lost. Bonnet (1945) now appears to be the only source (Peter Merrett pers. comm.).

Figure 2.—Martin Lister (birth not recorded, but baptized 1639, died 1712), a medic, is widely recognized as the "father of arachnology." In 1685, Lister was elected as vice president of the Royal Society under the president Samuel Pepys, in recognition of his achievements in natural history. His interests did not stop at spiders, and perhaps his greatest accolade was for his research in conchology. He recognized the value of fossils and was the first to attempt a comparative anatomy of the Mollusca in his "Exercitatio anatomica," "Historia sive synopsis methodica conchyliorum" and "Historia conchyliorum," which have received lasting recognition. However, although he made plenty of observations of spiders and other organisms, he did not complete any formal experiments and he is best described as a taxonomist, natural historian and intellectual. Source: Photo supplied by kind permission of Basil Harley and John Parker, the authors of "Martin Lister's English Spiders, 1678" published by Harley Books.

brations of a trapped fly; a basic example of a manipulation. However, Boys (1880) was unable to interpret the effect of the tuning fork, nor did he collect any worthwhile data to present. Boys (1880) is not unusual for his time, as many articles are of a similar type. For example, John Blackwall (Fig. 1), the renowned English arachnologist who first discovered the taxonomic importance of palps and epigyna, could also have been the founder of spider ecology. Writing between 1827–1877, Blackwall was an independent thinker and not one to conjecture. To the ecologist, he will be best known for attempting to unravel the mechanics of ballooning spiders which had captured the attention of a number of eminent scientists since the 17th century, most notably Martin Lister (1684) who recognized that it was silk that dragged spiders into the atmosphere (Fig. 2).

It was not until later that Bon de Saint-Hilaire (1710) described the forces that cause lift. However, there was also some fanciful

thinking that, for example, gossamer was the biproduct of evapotranspiration at harvest time or related to the vapors of the earth (Bechstein 1799). Blackwall was able to dismiss these and other nonsenses by experimentation (Blackwall 1827). He first described the tip-toe behavior and the "force" (i.e., drag) on the dragline which, through convection in the planetary boundary layer (which he termed "rarefraction of the air contiguous to the heated ground"), allowed spiders to become airborne. Rather ground breaking was the recognition that spiders have some limited control over their excursion, either drawing in the line or allowing more silk out, though previously Lister (1684) intimated that this might be a possibility. Despite these leaps of knowledge, Blackwall never presented any data or described even his experiments in sufficient detail that they could be replicated. He did refer to hypotheses, but there was certainly no evidence that these were formally tested and thus it is difficult to judge the validity of his claims. It is arguable that whilst Blackwall was clearly a man before his time, he did not practice science, but instead published observation with limited interpretation and may best be described as a natural philosopher and taxonomist.

It may seem harsh to judge Blackwall according to procedures of contemporary modern science, but in fact "modern deductive science" was practiced 150 years before Blackwall—see exhaustive treatment of the history of science in Gribbin (2002). Arguably, the first practitioner of modern deductive science was Isaac Newton. Newton experimented at the same time that Martin Lister was active in arachnology and both were fellows of the Royal Society at its inception in 1662. One can only speculate whether Newton and Lister actually ever met as fellows in the rooms of the Royal Society, it being a breeding ground for new ideas. Lister's big idea was that silk gave spiders lift, the number and length of the threads and the spider's posture determined whether they were to be "carried into the air by an external force" (Lister 1684 p. 593). To understand principles of "drag," which underpin ballooning, is complex and does require a rigorous understanding of Newtonian physics and a good manipulative experiment—Lister had neither. However, in terms of his thinking, Lister was a man before his time because, even in today's research world with the most sophisticated technology at our disposal and with over 300 years of Newtonian physics behind us, quantifying Lister's "external force" is at the cutting edge of current scientific discovery. We should reflect on the merits of Lister's work in terms of his ground-breaking work on the taxonomy and classification of spiders and shells (Fig. 2), accepting that he also made a philosophical, but not an experimental contribution to dispersal ecology.

That there was an absence of scientific ecological experimentation until the mid part of the 20th century is not to dismiss the fact that there were many good practitioners of natural history during and after Blackwall's period. Some of these individuals took the opportunity to publish beautifully illustrated taxonomic notes supplemented with limited aspects of spider behavior, many of which are now seen as "classics." These included the Reverend Octavius Pickard Cambridge ("Spiders of Dorset" published between 1879–1881), James Emerton ("The Common Spiders of the United States" published 1902), and latterly B.J. Kaston ("The Spiders of Connecticut" published 1948), W. Gertsch ("American Spiders" published 1949) and George Locket & Arthur Millidge ("British Spiders" published between 1951–1953). Others were more explicit about the natural history content, devoting most, if not all of their book to observation. These began in the latter half of the 19th century with Henry McCook ("American Spiders and their Spinning Work" published between 1889–1894), Eugene Simon ("Histoire Naturelle des Araignées" published between 1892–1903), Pelegrin Franganillo-Balboa ("Las Arañas" published 1917), E. Nielsen ("De Danske Edderkoppers Biologi" published 1928), Lucien Berland (*Les Araignées* published 1938) and William Bristowe ("The Comity of Spiders" published 1939–1941). Some authors were able to reach a wider market by popularizing their work to a mass audience. Arguably, this began with John Comstock and his "The Spider Book" (published 1913) and followed much later by K. McKeown ("Spider Wonders of Australia" published 1936) and John Crompton ("The Spider" published 1950). Good though their observations may seem, prudence suggests that intimate ecolog-

ical relationships are best described through a process of experimentation not just observation; the domain of journals not books.

Of all of the 8000+ papers in Bonnet's *Bibliographia Araneorum*, less than 0.1% of the journal papers mention the word "ecology" or its linguistic derivatives "ökologie/ecologie/ecologische/ekologitschni" in the title. Of those that do, it is evident that ecology as a discrete subject appeared in the first half of the 20th century (i.e., Shelford 1912; Adams 1915; Rau 1922, 1926; Weese 1924a, 1924b; Holmquist 1926; Peus 1928; Elliot 1930; Kolosváry 1930, 1933a, 1933b, 1937, 1938, 1939a, 1939b; Gebhardt 1932; Krogerus 1932; Ives 1934; Geijskes 1935; Kidd et al. 1935; Drensky 1936; Ksiazkowna 1936; Lever 1937; Petrusewicz 1938). One of the better papers of the above cohort is by Frank Elliott on spiders of a beech-maple forest published in 1930. Yet, this paper and all the aforementioned are nothing more than expanded field notebooks that include list upon list of spiders found in different strata or seasons. It is recognized that the early naturalists needed to lay foundations and simple principals to investigate the possibility of further testing. Yet, at the same time they had no focus, or apparent aim to their obsessional collecting sprees. While one can find merit in their observation, the lack of scientific rigor in the pre-1939 literature rarely invites close inspection for today's ecologists except to glean distribution and habitat data.

The lack of a scientific approach might be explained by the fact that only a few journals were dedicated to solely publishing ecological experiments, including "Ecology" (started 1920), "Zeitschrift für Morphologie und Ökologie der Tiere" (started 1924 but now known as Oecologia since 1968), "Ecological Monographs" (started 1931), "Journal of Animal Ecology" (started 1932) and later still, "Oikos" (started 1949). However, as has been evident throughout the screening process, finding a pre-1950s arachnological "experiment" worthy of publication in these international journals has been challenging.

One fundamental problem was that ecological concepts were rarely formalized until Charles Elton (Fig. 3), the so called "father of ecology," who laid the foundations for further testing. In his seminal 1927 book titled "Animal Ecology," Elton outlined several

Figure 3.—Charles Elton (1900–1991) was educated at New College Oxford where he immersed himself in zoology. The catalyst for his radical thinking was a product of an expedition to Spitsbergen in 1921, where he was struck by the contrasting life histories of many animals living there. Elton produced his seminal work titled "Animal Ecology" in 1927 in which he described his theory of the niche and his pyramid of numbers. Elton had much greater impact in arachnology than his predecessors. This is particularly true of the American Victor Shelford (1877–1968), who despite formalizing ecology as a discrete science, was rarely cited by arachnologists. Source: Photo supplied by Catherine Dockerty, Reader Services Librarian, Charles Elton Library, Department of Zoology, Oxford University, UK.

ecological ideas including food chains, nutrient cycles, ecological niches and the pyramid of numbers. If arachnologists had embraced these concepts and tested Elton's theories, then there would have been a plentiful supply of arachnological experiments worthy of international recognition. Instead, arachnologists set about producing a profusion of species lists, often without interpretation and making no attempt to relate their studies with current theory.

Interpretation of data is greatly aided by statistical inference, but statistics were absent from ecology until the turn of the 20th century. The lack of statistical methodology was perhaps the biggest frustration to the early ecologists who were unable to rationalize their findings. Arguably, the most significant advance in statistical ecology was the appointment of Ronald A. Fisher (Fig. 4) in 1922 to Rothamsted Experimental Station. Fisher, the architect of modern statistical field ecology,

Figure 4.—Sir Ronald Aylmer Fisher (1890–1962), was a eugenicist and friend of Leonard Darwin, son of Charles, who himself was the president of the Eugenics Education Society for which Fisher wrote many articles. However, he is best known for shaping our understanding of statistical research methods in ecology. Fisher enforced the view that experiments need to have both treatments and a control. Furthermore, he stated that these must be properly replicated and randomized, outlining his ideas in books aimed at field ecologists. He will be perhaps best remembered in statistics for the ANOVA, which was developed as a result of his work in genetics. The ANOVA was first used to show that the inheritance of continuous traits could be fully explained by a Mendelian model. This valuable tool was used by arachnologists in the 1950s and thereafter continuously until the present day. Source: Photo supplied by Gavin Ross, Rothamsted Research, UK.

developed statistical solutions to complex field experiments, such as the ANOVA, and laid down concepts such as maximum likelihood. Uniquely, he was able to formalize his approach in readable texts for biologists. His seminal works were "Statistical Methods For Research Workers" and "The Design of Experiments" first published in 1925 and 1935 respectively. While it is true that these two texts made an impact in some areas of ecology soon after they were published (e.g., botany and entomology), these texts did not feed into spider research until the 1950s (e.g., Barnes & Barnes 1955; Kuenzler 1958).

For some unknown reason, theoretical and statistical hindrances did not deter entomologists who were beginning to make significant inroads in insect science. Of particular fascination to entomologists at that time were competitive interactions and fluctuations in insect populations. Mathematical descriptions of the rhythmic fluctuations in animal populations had been available since the 1920s (Lotka 1925; Volterra 1926; Nicholson & Bailey 1935). Later, Crombie (1945, 1946) was one of the first to test the model on insects. Working with two species of grain beetle from the genera *Tribolium* (Coleoptera, Tenebrionidae) and *Oryzaephilus* (Coleoptera, Silvanidae), Crombie was able to measure the equilibrium population densities and competition coefficients to show that coexistence did occur at the predicted levels, thus validating his model. Similarly, Varley (1947) should also be mentioned for his scientific approach to the study of the knapweed gall-fly, *Urophora jaceana* (Hering 1935) (Diptera, Tephritidae), in which he was able to determine the density dependent factors which affected mortality. Ecology appeared to be alive and well in entomology (see Varley et al. 1973) but was suffering from poor health in arachnology. Spider ecology's deep malaise was only lifted by the intervention of a physiologist in 1939, although there were some encouraging philosophical beginnings after the turn of the 20th century.

The earliest ecological reference cited by David Wise (1993), the author of the only dedicated book on spider ecology, was Dahl (1906). Friedrich Dahl published over 60 papers on spiders between 1883–1927, but it was Dahl's (1906) paper on mating success that showed he could think along ecological lines, stating "there are no two species of indigenous spiders that occupy precisely the same position in nature's household" (quoted from Wise 1993). However, Dahl was a natural philosopher, a hypothesis generator, not a tester of his own ecological theories. Likewise, much the same could be said for Hermann Wiehle who studied the structure and function of the orb web for his PhD thesis at the University of Halle. He published continuously for nearly 50 years but 5 papers between 1927 and 1937, mostly for the journal

"Zeitschrift für Morphologie und Ökologie der Tiere," are notable (cited in Bonnet 1945). However, despite this prolific academic activity, Wiehle was only concerned with the construction of the web and its measurement, sadly ecology was never at the center of his observations (Samuel Zschokke pers. comm.). This is perhaps because Wiehle worked as a teacher and industrial worker after his PhD and had no resources to answer the ecological questions that must have arisen during his research. Questions regarding, for example, orientation and behavioral thermoregulation, would probably have been observed by Wiehle, although to answer these would have required a mathematical understanding, a good experiment and plenty of time. Two well executed examples came very much later. Both Pointing (1965) and Krakauer (1972) did have good experiments, but they were also reliant on the latest technology to make accurate temperature measurements. The level of accuracy allowed them to draw the same conclusion that web-spinning spiders use behavioral and physiological thermoregulation—something which Wiehle could not have concluded because of the lack of suitable apparatus and institutional support. However, Wiehle and his peers could have looked at simple habitat selection by web-spinning spiders and qualitatively noted the effect of independent variables (e.g., wind) in the same vein as Eberhard (1971) and Enders (1973). These were good but basic studies and ones that Wiehle and others could have executed; however, despite their obvious suitability, they did not appear until the 1960s.

Pontus Palmgren (Fig. 5), a distinguished Professor of Zoology at the University of Helsinki between 1940–1971, was best known for his anatomical research in ornithology (Koponen 1994). He was often heard repeating Galileo's motto "to measure everything and make the immeasurable measurable" (von Haartman 1994); this he applied rigorously to his work on the functional anatomy of bird's legs, spider muscles and trichobothria. Palmgren clearly enjoyed a diversity of disciplines, including ecology, publishing one scientific paper of note. Between finishing his PhD and his appointment to professorship, Palmgren turned his attention away from birds for a short while to investigate the ecology of a fishing spider in 1939.

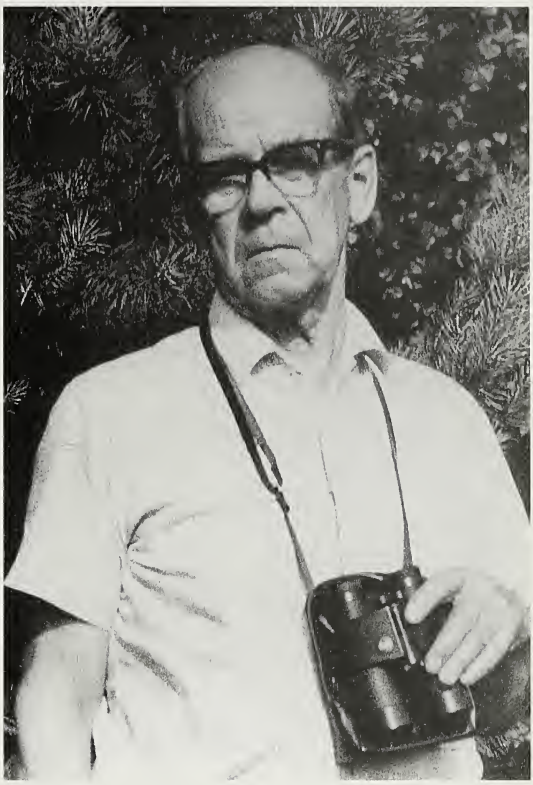


Figure 5.—Professor Pontus Palmgren (1907–1993), a physiologist who thought along ecological lines when trying to unravel the effect of environmental stimuli on *Dolomedes fimbriatus*. However, he will be best remembered for his groundbreaking work in ornithology, particularly that which relates to functional anatomy. Source: Photo supplied by kind permission of his son, Kaj Palmgren and with thanks to the Tvärminne Zoological Station, University of Helsinki, Finland.

Translated from its original German, Palmgren's (1939) paper was titled "Ecological and physiological studies concerning the spider *Dolomedes fimbriatus* (Clerck 1757) (Pisauridae)." It is immediately apparent that this paper is clearly a significant contribution to ecology. Furthermore, it is in the spirit of Ernst Haeckel's original definition of ecology that was seen as synonymous with physiology, a view espoused by the entomologist Victor Shelford and by others after the turn of the 20th century (McIntosh 1987). The paper includes a number of alternative hypotheses and manipulations both in the laboratory and the field. Palmgren (1939) demonstrated experimentally that *D. fimbriatus* was both positively phototaxic and negatively geotactic and

was aware that *Dolomedes* preferred damp habitats. However, while he could demonstrate physiologically that individuals dehydrate quickly through the skin, he was unable to explain why individuals did not orientate themselves towards saturated air in his behavioral experiments in the lab. Palmgren then studied individuals into the field where he investigated the consequences of habitat conditions on spider mortality. Placing individuals in cages (4 cm × 2 cm) in four different habitats (10 individuals per habitat) of increasing dampness (i.e., 1. open pine forest with dry heath (*Calluna vulgaris* (L.)); 2. hazel (*Corylus avellana* L.) copse; 3. moist mixed *Alnus glutinosa* (L.)-*Betula verrucosa* Ehrh. wood and; 4. a *Sphagnum* moss carpet with other marsh plants), he then measured the climatic conditions and lifespans of the spiders in each treatment. Palmgren (1939) was fascinated to observe that individuals placed in the bog had the longest lifespans, despite the climatic conditions remaining roughly the same between the four habitats. This he attributed to the fact that in the bog there was always a constant availability of water, although one wonders why, if this were true, he never recorded completely saturated air most of the time. It is suspected that if these measurements were repeated with modern data loggers, that the variance in humidity would be different between the bog and the dry heath and may have changed the course of his discussion slightly.

It is perhaps not surprising, given that this paper is written in German and not electronically indexed, that it is rarely cited by modern scientists. In one sense, this is a mistake because Palmgren (1939) was way ahead of his peers. However, Palmgren's (1939) experiments do not always stand up to modern-day scrutiny. The physiological measurements are satisfactory, and the only thing that would change if repeated today would be the technology and the numbers of replicates. However, it is the fieldwork where the reader is left wanting. As would be commonplace in any study of its kind, the first step would have been to present the numerical case for spiders appearing to have some kind of habitat association. This could have been done with simple density estimates from selected habitats. The second step would have been to design an experiment that allowed spiders to exploit their environment naturally, observing their behavior and the frequency of mortality. The idea that caged spiders are a field test of what was observed in the laboratory is idiosyncratic. Modern ecologists do confine wandering spiders, but the tendency is for them to use large semi-natural enclosures (i.e., $>1m^2$), not small cages (i.e., $8cm^2$).

It is clear to modern ecologists that Palmgren (1939) needed to make more connections between environment and spider mortality, which is suggestive of a correlation coefficient. The lack of statistical inference frustrated many ecologists including Shelford (1930, p. 236) who stated "often one sees papers containing weather data with no interpretation or correlation of the biological facts." However, even though correlations were used in ecological studies of the period (e.g., Nash 1933), they were by no means commonplace. For example, even under the supervision of Ronald Fisher, Barnes (1932) overlooked the importance of using any statistics at all to support his study on fluctuating insect populations, which is remiss. It is true that Palmgren's (1939) study would have been greatly improved by the use of correlations, but statistics were not part of the culture of the majority of ecologists of the period, and Palmgren cannot be chastised for this omission.

Ecological theory seemed more palatable than statistics to arachnologists and finally showed signs of making an impact, particularly Elton's (1927) theories of the niche and succession. Elton's theories became the preoccupations for post-war arachnologists (e.g., Gibson 1947; Lowrie 1948; Muma & Muma 1949; Dowdy 1951 and many others not included here). One notable Eltonite was an American named Robert Barnes who examined the ecology of spiders in non-forested maritime communities for his PhD at Duke University, North Carolina. Barnes produced three notable papers loosely centered around niche theory and distribution (Barnes 1953; Barnes & Barnes 1954, 1955). Arguably, Barnes' most cited paper is his 1955 work titled "The Spider population of the abstract broomsedge community of the southeastern Piedmont." This paper examined the spider community in terms of its homogeneity, density, population stability and range. Barnes used an ANOVA to form the view that of the 29 fields studied, the population structure was essentially the same—yet for all the paper's

merits, a hypothesis was lacking. Despite this and other papers of that time being good examples of basic ecology, they fail to make the relationship between environment and the spider community, because they did not try to control or manipulate the system, severely weakening their conclusions. Barnes could have tried to deconstruct the abstract community by manipulating the stand-type to see which species were specifically related to the structure or physiognomy of the broomsedge. By doing so, the ecology of the community would have been more clearly understood. The work of Barnes and others of the time illustrate that many "observational studies" were apparent and that the value of manipulation was not generally recognized until later.

Duffey (1956) was one of the first to include a basic manipulation in his paper on "The aerial dispersal of a known spider population," the subject of his PhD. For centuries, spiders had been observed ballooning, although it was not known what caused them to leave. Duffey set about attempting to understand the influence of population density and microclimate on ballooning success by using greased canes protruding from the sward of limestone grassland. While one can detect that Duffey excelled in the powers of observation, not all his conclusions are supported by his data. Fundamentally, Duffey should have manipulated the spider and microclimate and then, statements such as "temperature has a more important influence on aerial dispersal than have other microclimatic factors" (p. 111), could have be demonstrated probabilistically, not subjectively. Thus Duffey's (1956) paper pertains to be a basic manipulative experiment which does not explain how or why they balloon or shed light on their relationship with the habitat and its role in dispersal. Duffey published several other ecological papers which tended to be observational studies of conservation management appeal, rather than of academic scientific interest.

Edwin Nørgaard (Fig. 6), a Danish primary school teacher, published two ground-breaking papers in the journal Oikos which are still cited fifty years after their publication (Nørgaard 1951, 1956). It was these and other contributions which were of particular inspiration to Toft (2002) who elucidated upon Nørgaard's contribution to ecology in his opening address to the European Colloquium of Arachnology, Denmark 2000. Toft (2002) cited Nørgaard's first ecology paper in 1951 paper as "unprecedented in the scientific approach" and that Nørgaard "combined field observations with detailed laboratory experimentation, turn[ing] natural history into the experimental science of ecology." It is unequivocal that Toft (2002) believed that Nørgaard was the first arachnological ecologist, but he was not alone. The best textbook on animal ecology during the post war period, referred to Nørgaard's work as "outstanding" (Macfadyen 1966, p. 63).

Figure 6.—Edwin Nørgaard (1910-present) the modern day father of spider ecology who understood the value of experimental design. His two papers published in Oikos are seminal works and continue to be cited 50 years after their publication. Educated as a school teacher, Nørgaard did his fieldwork during school holidays, managing to maintain parallel interests in teaching and natural history. He wrote 39 papers, articles, books and book chapters over a period of 1936–1998 and was editor of the Danish journal "Flora og Fauna" for 30 years. Although he has retired, he still continues to write popular articles for the Natural History Mueum, Aarhus. Source: Søren Toft, University of Aarhus, Denmark. Photo supplied by E. Nørgaard.

In his first paper Nørgaard (1951) presented a suite of experiments which sought to examine the distributional ecology of two co-occurring lycosids in a sphagnum bog. His scientific rigor was evident by his thorough experimental examination and manipulation of the microclimate. Having made microclimatic field measurements in the different zones of the sphagnum, he did not conjecture that microclimate was determining the differences between the distribution of *Pardosa pullata* (Clerck 1757) and *Pirata piraticus* (Clerck 1757) (Lycosidae). Instead, he went into the laboratory to manipulate these variables and examine more closely their effect on the spiders. By doing so, he linked the lab to the field to erect a probable "cause and effect" scenario. He elucidated upon these findings at length to conclude that "there exists a clear correlation between the microclimate conditions of the habitats and the spider's requirements." Ideally, this statement needed underpinning with correlations between density estimates and average temperatures in the two layers of *Sphagnum*. Arguably, because there was an absolute zonation between the two species, density measurements could be viewed as redundant.

Nørgaard clearly demonstrated a scientific approach, but lacking in his first Oikos paper was an explicit hypothesis and a direct quantitative link to the environment. Implicit within his design was a statistical hypothesis statement that microclimate was predicted to be the cause of the distributions, written in the introduction as "differences in their distribution will be viewed in relation to the structure and microclimate of the sphagnum carpet." Nørgaard's (1956) second paper in Oikos on the environment and behavior of *Theridion saxatile* (now *Achaearanea riparia* (Blackwall, 1834)) (Theridiidae) is quite outstanding but in addition, an explicit hypothesis was clearly stated. Furthermore, Nørgaard's 1956 paper is an improvement on his 1951 publication because he also provided quantitative data on the distribution of the spider. He set out to investigate whether Nielsen's (1932) claim that *T. saxatile's* "egg cocoons are sometimes suspended somewhat below the nest to be sunned," was the real explanation of this behavior" (as quoted in Nørgaard (1956, p.160), itself a translation from Nielsen's Danish as found in his volume 1 on p. 189). Nørgaard (1956) took Nielsen's statement and made it his hypothesis and used it to design a suite of microclimatic experiments to test the role of temperature in the development and behavior of immature and adult spiders and their egg sacs. This eloquent set of experiments resulted in Nørgaard rejecting Nielsen's claim, instead accepting what was an alternative hypothesis that egg sac migration between 30–35 °C is an avoidance behavior to prevent thermally induced sub-lethal and lethal effects.

Nørgaard's achievements are best illustrated when they are compared with similar studies of that time, such as Shulov (1940) and Jones (1941). Shulov (1940) looked more generally at the effects of microclimate on the development in *Latrodectus tredecim-guttatus* (now *L. tredecimguttatus* (Rossi 1790)) and *L. pallidus* O. P.-Cambridge 1872 (Theridiidae) and Jones (1941) attempted to determine the effect of temperature and humidity on *Agelena naevia* (now *Agelenopsis naevia* (Walckenaer, 1842)) (Agelenidae). Both these papers are of an excellent high standard and they both manipulate the natural system. Where they both fail ecologically is that their experiments are purely laboratory based, and no data are taken from the field to support their laboratory measurements, although it should be noted that Shulov (1940) fills his paper with additional natural history notes. These papers illustrate the difference between biology which is "pure" and ecology which is "applied." In this respect, ecology has always strongly supported applied fieldwork over laboratory measurements made in isolation and without reference to nature (Shelford 1930). Pure biology does not impose this constraint necessarily, insofar as abstract physiological measurements are valid and need not be couched in terms of what actually happens in the field.

It has been observed that in reading many papers from the period up until 1956 that most were concerned with physiological effects on spiders, not population ecology which appeared to be leading the charge in entomology.

The literature between 1956 and 1973: did spider ecologists engage in science?.— The volume of papers and the number of journals accepting them accelerated after the Second World War. This post-war period has already been reviewed by Turnbull (1973) and

therefore it would be fruitless to re-review this period. Instead the purpose of this section is to examine whether the elegant experimentation that Nørgaard pursued was evident in others soon after 1956. To extend this trawl of the ecological literature up until the present day is beyond the scope of this review. Instead, although somewhat arbitrarily, I have chosen to confine my analysis of the literature to the actual publication date of Turnbull's 1973 review. However, in the case of Susan Riechert, where the author has had a single international publication footprint in the pre-1973 literature, I extend my search a little beyond the 1973 cut-off date because it is evident that she continues to have a lasting impact on spider ecology.

Of the 300+ papers treated by Turnbull, a minority relate to more general biological phenomena (e.g., the various headings detailing processes such as "spider silk and spinning organs;" "development," etc.), which are not strictly ecological and hence are not considered further. Of the papers reviewed that do pertain to ecology, the heading "population and community ecology of spiders" is by far the largest section, followed by those related to "spider feeding" and "webs." Very small sections refer to "survival and mortality," "reproduction," "energy flow" and "dispersal." Surprisingly, a section devoted to competition is absent.

An analysis of the literature cited in Turnbull (1973) reveals a number of authors who will still be familiar to students today. John Cloudsley-Thompson (1957), for example, wrote an excellent paper on the then valid genus *Ciniflo* (now *Amaurobius* C. L. Koch 1837) (Amaurobiidae). He worked to an explicit alternative hypothesis that nocturnal behavior in primitive spiders was the result of competition with more modern, successful diurnal species. Cloudsley-Thompson (1957) went further than Shulov (1940) and Jones (1941) before him, demonstrating elegantly the relations between microclimate and amaurobiids. However, Cloudsley-Thompson was a physiologist by his own admission and although he discussed his results in an ecological context (e.g., "the present work again stresses the importance of moisture on the distribution of spiders," pp. 150), he did not collect field data to support his analysis. Excellent though his work is, Cloudsley-Thompson's research is strictly physiological, of which there are many examples from the time (e.g., Lagerspetz & Jäynäs 1959; Miyashita 1968).

A number of authors continued to pursue "observational studies" in the post-1960s era, after the first wave of natural historians in the 1940s. This includes Turnbull's (1960) work on the stratification of spiders found in oak woods. This type of research, of which there are many, (e.g., Cherrett 1964; Duffey 1962, 1963, 1968; Huhta 1971; Sudd 1972) remains true to Elton's (1927) theory of the niche, but they are not an explicit test of it. Of considerable merit is the work of Sven Almquist (Fig. 7) who came much closer to understanding habitat selection than any of his peers, but who was completely overlooked by both Turnbull (1973) and by Wise (1993). Almquist, a Swede, studied at the University of Lund for his thesis titled "Habitat selection and spatial distribution of spiders in coastal sand dunes," which was submitted in 1973. Almquist married laboratory tests of microclimate (Almquist 1970, 1971) with field experiments of habitat selection and association (Almquist 1973a, b). In his 1973b paper, which includes a field test of his earlier laboratory measurements of temperature and humidity, he writes: "This paper deals with the correlations between the distribution of fifteen spider species of coastal sand dunes and the thermal tolerance and preference, and resistance to desiccation of each of those species under laboratory conditions" (p. 134)—an understated alternative hypothesis. Almquist worked in the spirit of Nørgaard's research on microclimate two decades earlier. Understandably due to technological advances, Almquist's measurements are much more accurate than Nørgaard's, but most striking is the level of detail that is given throughout his work which is not technologically driven. Generally, Almquist concludes his 1973b paper, having compared actual densities with climatic differences in the field and underpinned by his early manipulative microclimatic research in the lab, by stating ". . . habitat selection is fundamentally controlled by those requirements of the microclimate and the vegetation conditions. . . " In the same year, on a different dune system, the Dutch scientist van der Aart (1973) independently substantiated the conclusions of Almquist using what is believed to be the first example of ordination in

Figure 7.—Dr Sven Almquist (1918-present) wrote an exceptional set of ecological papers of spiders from Swedish sand dunes, which was the product of his 1973 PhD thesis from the University of Lund. Like Edwin Nørgaard, Dr. Almquist took up teaching. He retired from his post as senior master in biology at Malmö grammar School in 1983 after 37 years of service. Dr. Almquist started publishing in 1970 and has written 9 papers and published one popular Swedish language spider book. Although he continues to publish, his interests are confined to the systematics of Swedish spiders. His study of the systematics of Swedish spiders is the subject of his three volume *magnum opus*, the first volume of which will be published soon. Source: S. Almquist (with the help of University of Lund).

spider ecology, although this was 16 years after its first use in botany (Bray & Curtis 1957). Van der Aart (1973) used principal components analysis (PCA) to investigate whether the hypothesis of the multidimensional niche space was valid for a community of dune-living wolf spiders. PCA is now known to fail to meet the requirements of most ecological datasets, and van der Aart (1973) is guilty of over-interpretation of his results. However, many studies agree with van der Aart's (1973) main findings that differences exist between seaward and landward spider communities, and that the spatial distribution of spider species is linked to vegetation structure.

The re-appearing figure of Charles Elton suggests that he was an extremely influential thinker, not least for his contribution on the role of habitats in animal ecology. Elton's (1946) work is evident in Tretzel's (1952, 1954, 1955) theory-driven spider research concerning competition, maturity, reproduction and phenology. Tretzel is perhaps best known for his writings on interspecific competition, although this theory is not his own but appeared explicitly in Nicholson & Bailey's paper on the "Balance of animal populations" in 1935 and implicitly in Volterra's paper in 1926. Within spider ecology, Tretzel has some influence and spawned a number of studies over several decades (e.g., Vlijm et al. 1963; Łuczak 1966; Vlijm & Kessler-Geschiere 1967; Merrett 1967, 1968, 1969; Den Hollander 1971 among many others not cited here). Tretzel's view was that interspecific competition explained many of the differences observed between closely related species, including their temporal (e.g., phenology) and spatial distributions (e.g., habitat). An early exponent of Tretzel's work was Edward Kuenzler (1958) who published a paper on niche relations of three species of *Lycosa* (Lycosidae) in South Carolina. Using mark-recapture, Kuenzler (1958) presented habitat selection, density and home-range data as well as some limited meteorological comparisons to associate with spider activity. He showed that whilst the niche relations of *L. carolinensis* (now *Hogna carolinensis* (Walckenaer 1805)) and *L. timuqua* (now *Hogna timuqua* (Wallace 1942)) could not be separated, *L. rabida* (now *Rabidosa rabida* (Walckenaer 1837)) did not overlap with the other two species because it accessed the vertical component of the habitat, rather than just remaining on the ground or in its burrow. It is of note that Kuenzler's (1958) research does not include manipulation and his meteorological correlations are highly speculative, even though he was aware of Nørgaard's more clinical approach.

Kuenzler and other studies that are a test of Tretzel's work are a paradox: they show considerable merit because they are a test of ecological theory yet present no explicit hypotheses. One is left wondering why? It seems as if many of the population studies at the time

were hypothesis generating, as experiments were not a test of anything specific or at least anything that would suggest a hypothesis. This is not unusual, as McIntosh (1987) declares that "ecology, like biology, has commonly been criticized for its lack of an explicit and testable theoretical framework" (p. 257). For some reason, many of the population studies, which were in a similar vein to Kuenzler (1958), also chose lycosid spiders as their model organisms (e.g., Hackman 1957; Kajak & Łuczak 1961; Dondale et al. 1970; Kessler 1973). It is evident that there was a community of researchers working on lycosids who were interacting despite their disparate distribution across Northern Europe and America. Possibly because of the interaction and because lycosid spiders were a tractable model organism, a number of important advances in spider ecology materialized as a result of this research activity. It was relatively easy to demonstrate lycosid habitat choice in a simply designed natural experiment in grassland (e.g., Den Hollander & Lof 1972), but the many facets of habitat choice needed calibration and manipulation. Experiments of varying complexity showed that habitat choice provided a useful tool in explaining lycosid cannibalism (Hallander 1970), ballooning success (Richter 1967, 1970a, 1970b, 1971) frequency of feeding (Edgar 1970), reproductive rate (Richter et al. 1971) and courtship display (Hallander 1967), among others. While these studies should be noted, perhaps one lycosid study stands out above all other work for the period: Matthias Schaefer (Fig. 8) has been widely recognized as making a significant contribution to the study of spider competition and his work is exemplary. Schaefer's (1972) research involved six years studying eleven dominant lycosid species that occurred in 17 different coastal habitats. His major conclusion was that species were 'isolated' either in space or time. Schaefer hypothesized that abiotic influences were having a much greater effect than competitive displacement, despite evidence from his laboratory experiments which suggested that there were strong biotic interactions between species. In a re-analysis of Schaefer's work as summarized by Marshall & Rypstra (1999), Wise (1993) suggested that Schaefer was too conservative, in that he actually had compelling evidence of interspecific competition.

Figure 8.—Matthias Schaefer (1942-present) whose manipulative experiments concerning lycosid competition during the 1970s have been widely recognized as a significant contribution to the field. Matthias Schaefer has held a professorship at the Institute for Anthropology and Zoology, University of Göttingen since 1977. For the last 35 years, he has been an author of 131 scientific works spread across a broad research base. Notably, he has maintained a consistent and long standing interest in soil processes in beech forests, particularly that which relates to the involvement of invertebrates in the decomposition process. Source: Photo supplied by M. Schaefer.

Wise (1993) also revealed that, however good Schaefer's findings may be, it was unfortunate that there was an oversight in the experimental design: Schaefer lacked a properly replicated control. It is, perhaps, important to state that statistical probabilities can be undermined if the experimental design is not robust, as highlighted by Ronald Fisher. Fisher identified the problems of a lack of replication and the absence of a control in the 1920s when he was confronted with analyzing the Broadbalk experiment at Rothamsted Experimental Station (Gavin Ross pers. comm). The importance of experimental design was highlighted in Fisher's books designed for field-

workers, but it is frustrating to see that these problems still plagued notable and widely cited works during the 1960s and 1970s. Problems of replication can be found in Clarke & Grant's (1968) manipulative experiment which attempted to investigate role of spiders as predators in a beech-maple forest. Identified by Wise (1993) as a classic, the study used enclosures in which they removed spiders to observe the effect on Collembola, their likely prey. However, at the admission of the authors (p. 1154), the experiment was not properly replicated (3 controls, 1 treatment), and suffered from pseudoreplication (Wise 1993), still a hotly debated issue in ecology (Oksanen 2001, 2004; Hurlbert 2004).

Conversely, Eliza Dąbroska-Prot's experiments did not suffer from a lack of replication or control and were large in number. In 300 separate experiments, she, along with her colleagues Jadwiga Łuczak and Kazimierz Tarwid at the Institute of Ecology, Warsaw, investigated spider-mosquito predator-prey ratios in a series of five papers (Dąbroska-Prot 1966; Łuczak & Dąbroska-Prot 1966; Dąbroska-Prot et al. 1966, 1968). The group was aware of the theoretical background to their work making reference to Hollings disc equation (Dąbroska-Prot et al. 1968), a widely used theoretical approach to predator-prey interactions. However, for all its merits, their experimental methods are difficult to follow and I remain uncertain as to how the experiments proceeded and their justification for certain idiosyncrasies. For example, the team used isolators (enclosures) that followed a split-plot design in which both a control and a treatment were nested within a single enclosure, separated by a screen. There were ten such enclosures into which spiders and mosquitoes were added and observed three times a day over a period of six months. For some treatments with particular species they used 40 mosquitoes per plot and for others 50, whilst in the control there were always 50 mosquitoes. Concurrently, the team varied the numbers of spiders introduced inconsistently between species and not all spider introductions happened at the same time, with one species being added on the 8th day of the experiment and the rest at the beginning. I also cannot find evidence of the 300 experiments to which they refer, and am of the belief that the word experiment may be misused and intended to refer to a replicate*treatment*species combination. However, despite these flaws, I don't believe their major finding that wandering spiders exert more pressure on mosquitoes than sedentary web-spinning spiders is contentious.

Dąbroska-Prot manipulated the system to allow direct observation of prey consumption, but this has not always been possible. Spider researchers have for a long time been much more likely to use indirect methods to detect prey proteins in the gut, such as precipitin test. Its first use was in mosquito research in 1947; later this knowledge was applied to spiders in the study of the spruce budworm in 1963. As the 1980s approached, the precipitin test was being replaced by the enzyme linked immunosorbent assay (ELISA), but in this intervening period, researchers were also experimenting with radioactive isotopes. Moulder & Reichle (1972) used Cesium^{137} at the landscape scale, introducing the isotope to the forests of the Oak Ridge reservation in Tennessee, USA. The method of application is poorly described in the paper, but Auerbach et al. (1964) describe how this radioactive tracer was applied to a 20m × 25m stand of trees. Uptake occurred through the bark, using water as a diluent. The build-up of radiocesium was traceable in the leaves of the canopy of 33 trees. When the leaves fell onto the forest floor, decomposers then bioaccumulated the radioactive cesium and it was then passed on to any predator that consumed them. On the assumption that these were ground active predators, pitfall traps were used to catch spiders. As indicated by the researchers, C^{137} has a half-life of 30 years, which formed the justification for choosing this over the much less radioactive C^{134}. Cynics would suggest that spiders were a viable measure of how to monitor bioaccumulation of radioactive isotopes for the United States Atomic Energy Commission (USAEC) and that the paper's ecological significance was merely a byproduct of their findings. That said, this byproduct showed that trophic-level food-chain interactions could be measured and that spiders were important predators in forest ecosystems. However, Moulder & Reichle (1972) failed to demonstrate that the bioaccumulation of Cesium^{137} had little or no effect on spider behavior. This failing had implications on the estimates of rates of consumption of the prey and the subsequent catchability of the spiders in

the pitfall traps. If consumption rate and catchability were artifacts of the change in spider behavior following application of the tracer, the published data are likely to be a conservative estimate. The same criticism should be lodged at Van Hook (1971), in a related paper, who was also supported by the USAEC. Van Hook (1971) studied the uptake of the isotopes of calcium, potassium and sodium on a caged (0.25 m^2) grassland lycosid population. His energy flow diagrams are illuminating (e.g., fig. 7 in Van Hook (1971)), showing *Lycosa* at the top of the food chain and the interactions between it and its environment. However, the fundamental question remains, did the consumption of istope-tagged prey affect spider behavior? If so, then the study is drastically undermined.

David Quammen, widely recognized for popularizing ecology and biogeography, is in no doubt of the impact of one award winning experiment that is now "famous for its logical elegance, for its results and for its gonzo methods" (p. 428 Quammen 1996). There is further added praise from Lubchenco & Real (1991) in their review of classic papers in ecology, who suggested that it was "one of the most ambitious and successful large scale experiments attempted in ecological research" (p. 726). I am, of course, referring to the work of Dan Simberloff and Edward Wilson, who cast a shadow over all but a tiny portion of ecological research produced in the 1970s. Although spiders were not the specific focus of the work they, along with the rest of the arthropods collected, were a test of the equilibrium theory which was in need of empirical validation. Based in the Florida Bay, Simberloff and Wilson identified suites of mangrove islands which were each covered with a tent and 'defaunated' using methyl bromide fumigation (Simberloff & Wilson 1969; Wilson & Simberloff 1969). The fauna of six of these islands were censused before and after treatment, leading Simberloff & Wilson (1969) to conclude that recolonization curves approached a stable equilibrium with the exact number determined by the distance from the source habitats and the size of the island. Throughout, Simberloff & Wilson (1969) observed rapid species turnover and alluded to the fact that the majority of the fauna were "obligate transients," which were at the mercy of the wind. This includes a discussion of ballooning spiders in which it is highlighted that the distances could not be calculated or correlated with wind measurements because of a number of technical issues.

It would be remiss not to mention the work of Susan Riechert who published her first paper in 1972 and her first international paper in the following year. Riechert has been prolific in her publishing and her contribution to ecology cannot be underestimated. For example, her paper regarding thermal balance and prey availability in *Agelenopsis aperta* (Gertsch 1934) (Agelenidae) remains one of the few papers to attempt to unravel the complexities of spider-habitat associations (Riechert & Tracey 1975). Riechert has maintained a focus on *A. aperta* for the past 30 years, starting with her PhD work published in 1973. Riechert et al.'s (1973) paper was not a manipulative experiment in itself, but it was well designed and presented a strong case to suggest that spiders and their habitat were correlated. What is apparent in retrospect was that her PhD research laid the groundwork for a multitude of studies which had a strong manipulative component and solid theoretical background. A monograph on the contribution of Susan Riechert is long overdue and would be extremely rewarding (but see Wise 1993 for a detailed overview of her research up until the early 1990s). Two other "appearing lights" beginning their research at the same time as Riechert were Frank Enders and William Eberhard whose work on web-site selection is still widely read today, and who began publishing their mainstream work in the early 1970s. I refer readers to Wise (1993) and to specific reviews on web-site selection for a proper treatment of their work, most of which extends beyond the cut-off date for this review.

To summarize the period of 1956–1973, there was a profusion of literature that did not engage science, but pursued an often circular interest of basic observational studies. Fundamentally, these often fell short of the scientific approach because they did not manipulate the system, or if they did, they manipulated to the wrong component. These studies are still informative but they must be treated with caution as some findings sway in the favor of conjecture, not substantive probability. For example, Chew's (1961) natural experiment is a small study of spiders (n = 817 individuals) of a desert community. Sur-

prisingly, it is still widely cited but is, in my view, erroneous. There are errors in the standardization of the sampling regime and wild conjectural statements made in the discussion which are unsupported by a formal analysis and an evidence-based manipulation (e.g., the role of temperature). When done well, observational studies are an extremely valuable resource to ecologists. Robinson & Robinson's (1973) study of the giant wood spider *Nephila maculata* (now *Nephila pilipes* (Fabricius 1793)) (Tetragnathidae), illustrates this point precisely. It is complete in its approach and does not suffer the illusion that it is anything other than a hypothesis generating autecological paper.

An overview of the literature sampled.—If I were to summarize what impact most of the papers included in this review have had on ecology, then I could do no better than to quote Turnbull's (1973, p. 333) synopsis of over 300 "ecological" studies: "I wish I could also say that I had found no shortage of good papers, or good, well supported information on spider ecology. There are some excellent papers, but there are also large quantities of repetitious mediocrity. I am dismayed at the number of papers that, if they do not belong in ecology do not belong anywhere. [These papers] . . . leave me wondering why they were written, or if written, why any journal would publish them. They are often the product of the crudest methodology; they present data sets that cannot be analyzed; they come to no conclusions; and they are not put into any sort of relationship with general principles, ecological or otherwise." While I appreciate that spider ecology needed to go through a period of evolution, it is surprising that the mediocrity prevailed for so long and that the revolution appeared as late as the mid-twentieth century. Arguably, Turnbull did not expedite the rise of spider ecology by publishing cutting-edge research himself. Instead, he could be accused of being no different from his peers, in that his work was neither remarkable nor original; for those qualities, spider ecologists need to look to elsewhere.

Rainer Foelix, author of the "Biology of Spiders", wrote in the opening lines of his ecological chapter "the interactions between spiders and their environment have been investigated systematically only within the past few decades" (Foelix 1982, p. 232). If there was a need to be more exact, it is argued that arachnological ecology began with Pontus Palmgren in the late 1930s and was refined in the mid 1950s by Edwin Nørgaard with his experiments of microclimate. Both men understood that to manipulate the system is to understand the relationships between spiders and their environment more clearly. Edwin Nørgaard built on the experiences of Pontus Palmgren who worked in the spirit of Haeckel's physiological definition of ecology. However, Nørgaard's work was exemplary because he recognized the need to make both field and controlled laboratory observations. Sven Almquist and Matthias Schaefer also recognized the elegance of manipulation and their work is exceptional for the period.

CONCLUDING REMARKS

Spider research and experimental design.—I hope that through the course of this review, I have managed to convey at least two things: the power of hypothesis testing and the need for a manipulation of either the habitat or the spider, and sometimes both. I would like to encourage students in all branches of arachnology to consider the value of manipulative experiments that are part of a well planned design, and to move away from pure faunistics, which is provincial and therefore of little value. Furthermore, while I recognize that hypotheses are not always appropriate (e.g., when there are provisional data) and that when used imprecisely they seem rather drab, detectable hypothesis statements add a great deal of depth to most experimental designs. These statements need not be of the null form, but can include multiple dynamic alternatives.

Spider research and ecological theory.—It is evident that most studies included in this review had only a peripheral interest in testing ecological theory. This explains why spider ecology was in the doldrums and remained inward-looking during a period when other disciplines embraced the interaction between theory, experiments and empirical tests. For example, it has been argued by Statzner et al. (2001) that entomology has generated a number of general theories in ecology, but that botany has made the most significant contributions. Perhaps one of the most notable theories that has come directly from entomology and which had general appeal to ecologists is the Habitat Templet by the entomologist T.R.E

Southwood (1977). More recently, Ilka Hanski has had a similar impact with his Theory of Metapopulations derived from extensive butterfly studies (Hanski 1999). While it is easy to demonstrate the positive impact spider research has had on other science disciplines such as biochemistry (e.g., spider silks feeding into our understanding of arthropod silks and their evolution), it is difficult to find a single example where this has happened in ecology pre-1973.

I have consulted fellow scientists in numerous countries on the thorny issue of the impact of spider research on other science disciplines. International scientists were even asked if they could give an example of a theory that was not restricted by the 1973 cut-off date—none were forthcoming. Why should this be so? During the embryonic phase of spider ecology, it could be argued that spiders were dealt with as a second taxon to the insects. Indeed, whereas entomologists were likely to be snapped up by institutions wishing to employ them, arachnologists were not. It is also evident that communication between research groups and individuals was poor. For example, it has been observed by scientists both sides of the English Channel that, due to language barriers, papers written in anything other than the mother tongue of the author were largely ignored. All these factors would have meant that an exchange of hypotheses were all the more difficult. We know that hypotheses drive theory and thus theoretical spider ecology must have suffered as a result.

But what is our excuse now that we are in the 21st century? We meet regularly at conferences, congresses and seminars and for some of the ecology journals we even have pre-publication access to papers as well as a wealth of electronic media and back issues. Furthermore, spiders are well distributed, often in abundance and available for study throughout much, sometimes all of the year. It is not as if we do not have our hand on the pulse or have an obliging model organism. It seems to me as if there are no big questions in ecology which pre-dispose spiders to scientists in the search for their big ideas. Perhaps this is because we still do not know enough about our commonest spiders that would encourage sceptics to take a closer look. That was certainly true in agriculture as it has only been in the last three decades that spiders have stopped hiding behind the large, looming shadow of insect economic entomology and branched out in to the collective that is now known as "beneficial predators." Howell & Pienkowski (1971), for example, give a short breakdown of experimental studies of spiders in American agriculture and show that, apart from a limited number of studies in sweet corn, sugarcane, sorghum and cotton, spider studies are otherwise absent. Post-second millennium, much has changed and there are now numerous groups around the world solely researching the role of spiders in agriculture.

I do believe that the lack of a new general theory applicable to ecology will not last for much longer. The reason for this confidence is because Susan Riechert (pers. comm.) has argued that, although spiders have not initiated new theory, they have proved important experimental subjects that have given support to our understanding and driven further general ecological developments. Thus, we are very theoretically aware and it is encouraging to find that we use theory in our research with some frequency. It is only the contribution to general ecology that we are lacking, so what could we do to encourage this? What to me seems critical is that we interact at the highest level, find paradigms of general applicability and do not present ourselves as a phylogenetic cul-de-sac where no one wants to stop and visit. Then, and only then will spider ecology cross over into general ecology in a major way.

What of the future of experimental spider ecology?.—Unlike physics, ecological relationships are difficult to define absolutely, which explains our addiction to statistical methods, but not necessarily to probabilistic tests. Spider researchers, like other ecologists, are confronted with a complex world of interactions that they have to untangle systematically. The traditional null hypothesis approach does not serve ecology well when complexity in nature is not met with complexity in statistical theory. It is now argued by an increasing band of ecologists, that null hypothesis testing should be curtailed and the use of P-values questioned when established via traditional approaches in some circumstances (Johnson 1999; Anderson et al. 2000; Eberhardt 2003; Johnson & Omland 2004). These authors propose an alternative called "model selection"

(MS) which allows up to 20 multiple competing hypotheses to be weighted and compared. Model selection allows the possibility that more than one hypothesis might be true, allowing the researcher to rank their importance and identify more than one outcome (Johnson & Omland 2004). This is in stark contrast to the rather simple dichotomy of null hypotheses testing. I can find only one example where MS has been used in arachnology, in which the ecological traits of phytoseiid mites were assessed (Luh & Croft 1999). However, the likely outcome is that MS will become more prevalent in spider research, especially in the study of trophic relations and competition. However, I do not believe that, where clear and considered manipulations are possible, MS can ever replace manipulative experiments given that MS is founded on observational data mathematically expressed. Experimental ecology is here to stay and at the center of its development is manipulation, albeit somewhat scaled-up to what our forebears had in mind.

ACKNOWLEDGEMENTS

The views expressed here are my own and not necessarily supported by those from whom I have sought help. This paper has been six years in the making, but its relevance was crystallized as a result of discussions first with Margaret Hodge (USA) and subsequently with Søren Toft (Denmark) who fuelled my enthusiasm to look more closely. I am extremely grateful to the two anonymous referees who have improved the manuscript and presented an alternative view. I am appreciative to Emma Shaw (UK) for her help and thank Søren, Gernot Bergthaler (Austria), and Samuel Zschokke (Switzerland) for translations. Phil Wheater (UK), Gary Miller (USA) and Susan Riechert (USA) are thanked for their suggestions. I also thank Chris Felton (UK) and the British Arachnological Society library for providing me with translated reprints of Tretzel's work and Peter Merrett (UK) and Robert Suter (USA) for information. For photographic portraits, I acknowledge the help of Søren Toft, University of Aarhus (Denmark), Basil Harley (UK), John Parker (UK), Jamie Owen of the Natural History Museum, London (UK), Gavin Ross, Rothamsted Research (UK), University of Lund (Sweden), Sven Almquist (Sweden), Kaj Palmgren through the help of the Tvärminne Zoological Station, University of Helsinki (Finland). Thanks to Alison Haughton for proof reading the MS.

LITERATURE CITED

Aart, P.J.M. van der. 1973. Distribution analysis of wolf spiders (Araneae, Lycosidae) in a dune area by means of principal component analysis. Netherlands Journal of Zoology 23:266–329.

Adams, C.C. 1915. An ecological study of prairie and forest invertebrates. Bulletin of the Illinois State Laboratory of Natural History 11:31–280.

Almquist, S. 1970. Thermal tolerances and preferences of some dune-living spiders. Oikos 21: 230–236.

Almquist, S. 1971. Resistance to desiccation in some dune-living spiders. Oikos 22:225–229.

Almquist, S. 1973a. Habitat selection by spiders on coastal sand dunes in Scania, Sweden. Entomologia Scandinavica. 4:134–154.

Almquist, S. 1973b. Spider associations in coastal sand dunes. Oikos 24:444–457.

Anderson, D.R., K.P. Burnham & W.L. Thompson. 2000. Null hypothesis testing: problems, prevalence and an alternative. Journal of Wildlife Management 64:912–923.

Auerbach, S.I., J.S. Olson & H.D. Waller. 1964. Landscape investigations using cesium-137. Nature 201:761–764.

Barnes, H.F. 1932. Studies of fluctuations in insect populations: I. The infestation of Broadbalk wheat by the wheat blossom midges (Cecidomyiidae). Journal of Animal Ecology 1:12–31.

Barnes, R.D. 1953. The ecological distribution of spiders in non-forested maritime communities at Beaufort, North Carolina. Ecological Monographs 23:315–337.

Barnes, B.M. & R.D. Barnes. 1954. The ecology of the spiders of maritime drift lines. Ecology 35: 25–35.

Barnes, R.D. & B.M. Barnes. 1955. The spider population of the abstract broomsedge community of the southeastern piedmont. Ecology 36:658–666.

Bechstein, J.M. 1799. Observations on the true origin of the gossamer. Philosophical Magazine. London. 4:119–124.

Berland, L. 1938. Les Araignées. Paris 1938:1–175.

Blackwall, J. 1827. Observations and experiments made with a view to ascertain the means by which the spiders that produce gossamer effect their aerial excursions. Transactions of the Linnaean Society of London 15:449–459.

Bon de Saint-Hilaire, F.X. 1710. On the usefulness of the silk of spiders. Philosophical Transactions of the Royal Society of London 27:2–15.

Bonnet, P. 1945. Bibliographia Araneorum. Analyse méthodique de toute la literature aranéologique Jusqu'en 1939. Tome 1. Toulouse, Les Frères Douladoure.

Boys C.V. 1880. The influence of the tuning-fork on the garden spider. Nature 23:149–150.

Bray, J.R. & J.T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27:325–349.

Bristowe, W.S. 1939. The Comity of Spiders. Ray Society, London, vol. 1.

Bristowe, W.S. 1941. The comity of spiders. Ray Society, London, vol. 2.

Cambridge, O.P.-. 1879. The spiders of Dorset. Araneidea. Proceedings of the Dorset Natural History Field Club 1:1–235.

Cherrett, J.M. 1964. The distribution of spiders on the Moor House National Nature Reserve, Westmorland. Journal of Animal Ecology 33:27–48.

Chew, R.M. 1961. Ecology of the spiders of a desert community. Journal of the New York Entomological Society 69:5–41.

Clarke, R.D. & P.R. Grant. 1968. An experimental study of the role of spiders as predators in a forest litter community. Part 1. Ecology 49:1152–1154.

Clerck, C. 1757. *Svenska spindlar, uti sina hufvudslågter indelte samt under några och sextio särskildte arter beskrefne och med illuminerade figurer uplyste.* Stockholmiae, 154 pp.

Cloudsley-Thompson, J.L. 1957. Studies in diurnal rhythms. V. Nocturnal ecology and water relations of the British cribellate spiders of the genus *Ciniflo* Bl. Journal of the Linnean Society of Zoology 43:134–152.

Comstock, J.H. 1913. The Spider Book. Garden-City, N.Y.

Connor, E.F. & D. Simberloff. 1986. Competition, scientific method, and null models in ecology. American Scientist 74:155–162.

Cottenie, K. & L. De Meester. 2003. Comment to Oksanen (2001) : reconciling Oksanen (2001) and Hurlbert (1984). Oikos 100:394–396.

Crombie, A.C. 1945. On competition between different species of graminivorous insects. Proceedings of the Royal Society B. 132:362–395.

Crombie, A.C. 1946. Further experiments on insect competition. Proceedings of the Royal Society B. 133:76–109.

Crompton, J. 1950. The Spider. Nick Lyons Books, New York.

Dąbroska-Prot, E. 1966. Experimental studies on the reduction of the abundance of mosquitoes by spiders. II Activity of mosquitoes in cages. Bulletin de L'Acadêmie Polonaise des Sciences CL II 14:771–775.

Dąbroska-Prot, E., J. Łuczak & K. Tarwid. 1966. Experimental studies on the reduction of the abundance of mosquitoes by spiders. III Indices of prey reduction and some controlling factors. Bulletin de L'Acadêmie Polonaise des Sciences CL II 14:777–782.

Dąbroska-Prot, E., J. Łuczak & K. Tarwid. 1968. Prey and predator density and their reactions in the process of mosquito reduction by spiders in field experiments. Ekologia Polska. Seria A 16: 773–819.

Dahl, F. 1906. Die physiologische Zuchtwahl im weiteren Sinne. Biologisches Zentralblatt 26:3–15.

Den Hollander, J. 1971. Life histories of species in the *Pardosa pullata* group, a study of ten populations in the Netherlands (Araneae, Lycosidae). Tijdschrift voor Entomologie 114:255–281.

Den Hollander, J. & H. Lof. 1972. Differential use of habitat by *Pardosa prativaga* (L. Koch) and *Pardosa pullata* (Clerck) in a mixed population (Araneae: Lycosidae). Tijdschrift voor Entomologie 115:205–215.

Dondale, C.D., J.H. Redner, E. Farrell, R.B. Semple & A.L. Turnbull. 1970. Wandering of hunting spiders in a meadow. Bulletin Du Museum National D'Histoire Naturelle 41:61–64.

Dowdy, W.W. 1951. Further ecological studies on stratification of the arthropods. Ecology 32:37–52.

Drensky, P. 1936. Izoutschwania weurchou paiatzite na beulgaria I technite ekologitschni I biogeografski osobenosti. Troudowe Na Beulgarskoto Pirodoiznitatelno Proujestwo 17:71–115.

Duffey, E. 1956. Aerial dispersal in a known spider population. Journal of Animal Ecology 25:85–111.

Duffey, E. 1962. A population study of the spiders in limestone grassland. Description of the study area, sampling methods and population characteristics. Journal of Animal Ecology 31:571–599.

Duffey, E. 1963. Ecological studies of the spider fauna of the Malham Tarn area. Field Studies 1: 65–87.

Duffey, E. 1968. An ecological analysis of the spider fauna of sand dunes. Journal of Animal Ecology 37:641–674.

Eberhard, W.G. 1971. The ecology of the web of *Uloborus diversus* (Araneae: Uloboridae). Oecologia 6:328–342.

Eberhardt, L.L. 2003. What should we do about hypothesis testing? Journal of Wildlife Management 67:241–247.

Edgar, W.D. 1970. Prey and feeding behaviour of adult females of the wolf spider *Pardosa amentata* (Clerck). Netherlands Journal of Zoology 20:487–491.

Elliot, F.R. 1930. An ecological study of spiders of the beech-maple forest. Ohio Journal of Science 30:1–22.

Elton, C. 1927. Animal Ecology. Sedgewick & Jackson, London.

Elton, C. 1946. Competition and the structure of animal communities. Journal of Animal Ecology 15:54–68.

Emerton, J.H. 1902. The common spiders of the United States. Boston.

Enders, F. 1973. Selection of habitat by the spider *Argiope aurantia* Lucas (Araneidae). American Midland Naturalist 90:47–55.

Fisher, R.A. 1925. Statistical Methods for Research Workers. Oliver and Boyd, London.

Fisher, R.A. 1935. The Design of Experiments. Oliver and Boyd, London.

Foelix, R.F. 1982. The Biology of Spiders. Harvard University Press, Cambridge.

Franganillo B., P. 1917. Las Arañas. Manual de Araneología, Gijón.

Gebhardt, A. 1932. Ökologiai és faunisztikai vizsgálatok a zenoga medencében. Állatani Közlemények 29:42–59.

Geijskes, D.C. 1935. Faunistisch-ökologische Untersuchungen am Roserenbach bei Liestal im Basler Tafeljura. Tijdschrift voor Entomologie 78:249–382.

Gertsch, W.J. 1979. American Spiders. Van Nostrand Co., New York.

Gibson, W.W. 1947. An ecological study of the spiders of a river terrace forest in western Tennessee. Ohio Journal of Science 47:38–44.

Gribbin, J. 2002. Science: a history 1534–2001. Penguin Books, London.

Hackman, W. 1957. Studies on the ecology of the wolf spider *Trochosa ruricola* Deg. Societas Scientiarum Fennica. Commentationes Biologicae 16:1–34.

Haeckel, E. 1866. Generelle Morphologie der Organismen. Berlin, Georg Reimer, 2 volumes.

Hairston, N.G. 1989. Ecological Experiments. Cambridge University Press, Cambridge.

Hallander, 1967. Range and movements of the wolf spiders *Pardosa chelata* (O.F. Müller) and *Pardosa pullata* (Clerck). Oikos 18:360–364.

Hallander, H. 1970. Prey, cannibalism and microhabitat selection in wolf spiders *Pardosa chelata* (O.F. Müller) and *Pardosa pullata* (Clerck). Oikos 21:337–340.

Hanski, I. 1999. Metapopulation Ecology. Oxford University Press, Oxford.

Holmquist, A.M. 1926. Studies in arthropod hibernation. I. Ecological survey of hibernating species from forest environments of the Chicago region. Annals of the Entomological Society of America 19:395–426.

Howell, J. O. & R.I. Pienkowski. 1971. Spider populations in alfalfa, with notes on spider prey and effect of harvest. Journal of Economic Entomology 64:163–168.

Huhta, V. 1971. Succession in the spider communities of the forest floor after clear cutting and prescribed burning. Annales Zoologici Fennici 8: 483–542.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54:187–211.

Hurlbert, S.H. 2004. On misinterpretations of pseudoreplication and related matters: a reply to Oksanen. Oikos 104:591–597.

Ives, J.D. 1934. Notes on the fauna and ecology of Tennessee caves. Journal of the Tennesee Academy of Sciences 9:149–153.

Jackson, R.R., S.D. Pollard, X.J. Nelson, G.G. Edwards & A.T. Barrion. 2001. Jumping spiders (Araneae: Salticidae) that feed on nectar. Journal of Zoology London 255:25–29.

Johnson, D.H. 1999. The insignificance of statistical significance testing. Journal of Wildlife Management 63:763–772.

Johnson, J.B. & K.S. Omland. 2004. Model selection in ecology and evolution. Trends in Ecology and Evolution 19:101–108.

Jones, S.E. 1941. Influence of temperature and humidity on the life history of the spider *Agelena naevia* Walckenaer. Annals of the Entomological Society of America 34:557–571.

Kajak, A. & J. Łuczak. 1961. Clumping tendencies in some species of meadow spiders. Bulletin de L'Acadêmie Polonaise des Sciences CL II 9:471–476.

Kaston, B. J. 1948. Spiders of Connecticut. Bulletin of the Connecticut State Geological and Natural History Survey. 70:1–874.

Kidd, F.L., K.A. Pyefing & P.M. Butler. 1935. The ecology of Bardsey island: topography and types of environment. Journal of Animal Ecology 4: 231–243.

Kessler, A. 1973. A comparative study of the production of eggs of eight *Pardosa* species in the field (Araneae, Lycosidae). Tijdscrift voor Entomologie 116:23–41.

Kolosváry, G. 1930. Ökologische und biopsychologische Studien über die Spinnenbiosphäre der gesamten Halbinsel von Tihany. Zeitschrift Morphologie und Ökologie Tiere 19:493–533.

Kolosváry, G. 1933a. Ökologiai kutatásaim a bükk hegység barlangjaiban. Barlangvilág 3:6–13.

Kolosváry, G. 1933b. Beiträge zur Faunistik und Ökologie der Tierwelt der ungarländdischen Juniper eten. Zeitschrift für Morphologie und Ökologie der Tiere 28:52–63.

Kolosváry, G. 1937. Studi ecologico-faunistici nella pannonia meridionale Ungheria. Rivista Di Biologia 23:3–15.

Kolosváry, G. 1938. Über die Ergebnisse meiner spinnen-ökologischen Forschungen in Rovigno Folia Entomologica Hungarica 4:39–46.

Kolosváry, G. 1939a. Ein ökologischer Vergleich zwischen der Spinnenfauna der Kecshe- und der Stephans-Höhle in Ungarn. Folia Zoologica et Hydrobiologica 9:334–337.

Kolosváry, G. 1939b. Über die Bedeutung der ökologisch-biocönotischen Forschungen an kleinen

Terrains. Folia Zoologica et Hydrobiologica 9: 345–348.
Koponen, S. 1994. In memoriam. Pontus Palmgren 1907–1993. Bulletin d'information et de liaison du Centre International de Documentation Arachnologique 11:3.
Krakauer, T. 1972. Thermal responses of orb-weaving spider, *Nephila clavipes* (Araneae-Argiopidae). American Midland Naturalist 88:245–250.
Krogerus, R. 1932. Über die Ökologie und Verbreirung der Arthropoden der Triebsandgebiete an den Küsten Finnlands. Acta Zoologica Fennica 12:1–308.
Ksiazkowna, I.H. 1936. Charakterystyka ekologicznych zespolópajaów pajaków w lasach pogórza cieszyńskiego. Wydawnictwa Slaskie Prace Biologiczne 1:131–161.
Kuenzler, E.J. 1958. Niche relations of three species of lycosid spiders. Ecology 39:494–500.
Lagerspetz, K. & E. Jäynäs. 1959. The behavioural regulation of the water content in *Linyphia montana* (Aran. Linyphiidae) and some other species. Annales Entomologici Fennici 25:210–233.
Lever, R.J.A.W. 1937. A contribution to the ecology of a grassland community on Guadacanal Island, British Soloman Islands Protectorate. Journal of Animal Ecology 6:291–297.
Lister, M. 1684. On the projection of the threads of spiders, and on bees breeding in cases made of leaves, as also, a viviparous fly. Philosophical transactions of the Royal Society London 14: 592–596.
Locket, G.H. & A.F. Millidge. 1951. British Spiders, Vol. I. Ray Society, London.
Locket, G.H. & A.F. Millidge. 1951. British Spiders, Vol. II. Ray Society, London.
Lotka, A.J. 1925. Elements of Physical Biology. Williams and Wilkins, Baltimore.
Lowrie, D.C. 1948. The ecology of the spiders of the xeric dunelands in the Chicago area. Bulletin of the Academy of Sciences 6:161–189.
Lubchenco, J. & L.A. Real. 1991. Manipulative experiments as tests of ecological theory. Pp. 715–733. *In* Foundations of Ecology: classic papers with commentaries. (L.A. Real & J.H. Brown eds.). University of Chicago Press, Chicago.
Łuczak, J. 1966. The distribution of wandering spiders in different layers of the environment as a result of interspecies competition. Ekologia Polska—Seria A 14:233–244.
Łuczak, J. & E. Dąbroska-Prot. 1966. Experimental studies on the reduction of the abundance of mosquitoes by spiders. I. Intensity of spider predation on mosquitoes. Bulletin de L'Acadêmie Polonaise des Sciences CL II 14:315–320.
Ludy, C. 2004. Intentional pollen feeding in the spider *Araneus diadematus* Clerck, 1757. Newsletter of the British Arachnological Society 101:4–5.
Luh, H.K. & B.A. Croft. 1999. Classification of generalist or specialist life styles of predaceous phytoseiid mites using a computer genetic algorithm, information theory, and life history traits. Environmental Entomology 28:915–923.
Macfadyen, A. 1966. Animal Ecology. Sir Isaac Pitman & Sons Ltd., London.
Marshall, S.D. & A.L. Rypstra. 1999. Spider competition in structurally simple ecosystems. Journal of Arachnology 27:343–350.
McCook, H.C. 1889. American spiders and their spinningwork. Philadelphia 1:1–373.
McCook, H.C. 1890. American spiders and their spinningwork. Philadelphia, 2:1–480.
McCook, H.C. 1894. American spiders and their spinning-work. Philadelphia 3:1–285
McIntosh, R.P. 1987. The Background to Ecology. Cambridge University Press, Cambridge.
McKeown, K.C. 1936. Spider Wonders of Australia. Sydney
Merrett, P. 1967. The phenology of spiders on heathland in Dorset. I. Families Atypidae, Dysderidae, Gnaphosidae, Clubionidae, Thomisidae and Salticidae. Journal of Animal Ecology 36: 363–374.
Merrett, P. 1968. The phenology of spiders on heathland in Dorset. Families Lycosidae, Pisauridae, Agelenidae, Mimetidae, Theridiidae, Tetragnathidae, Argiopidae. Journal of Zoology (London) 156:239–256
Merrett, P. 1969. The phenology of linyphiid spiders on heathland in Dorset. Journal of Zoology (London) 157:289–307.
Miyashita, K. 1968. Growth and development of *Lycosa T-insignita* Boes. et Str. (Araneae: Lycosidae) under different feeding conditions. Applied Entomology and Zoology (Tokyo) 3:81–88.
Moulder, B.C. & D.E. Reichle. 1972. Significance of spider predation in the energy dynamics of forest-floor arthropod communities. Ecological Monographs 42:473–498.
Muma, M.H. & K.E. Muma. 1949. Studies on the population of prairie spiders. Ecology 30:485–503.
Murray, B.G.Jr. 2001. Are ecological and evolutionary theories scientific? Biological Reviews 76:255–289.
Nash, T.A.M. 1933. A statistical analysis of the climatic factors influencing the density of Tsetse flies, *Glossina morsitans* Westw. Journal of Animal Ecology 2:197–203.
Nicholson, A. J. & V.A. Bailey. 1935. The balance of animal populations. Proceedings of the Zoological Society of London 3:551–598.
Nielsen, E. 1928. De danske Edderkoppers Biologi. (J. P. Kryger, 1929) 16:319–322.
Nielsen, E. 1932. The Biology of Spiders. Vols I and II. København
Nørgaard, E. 1951. On the biology of two lycosid

spiders *Pirata piraticus* and *Lycosa pullata* from a Danish sphagnum bog. Oikos 3:1–21.

Nørgaard, E. 1956. Environment and behaviour of *Theridion saxatile*. Oikos 7:159–192.

Oksanen, L. 2001. Logic of experiments in ecology: is pseudoreplication a pseudoissue? Oikos 94: 27–38.

Oksanen, L. 2004. The devil lies in the details: reply to Stuart Hurlbert. Oikos 104:598–605.

Palmgren, P. 1939. Ökologische und physiologische Untersuchungen über die Spinne *Dolomedes fimbriatus* Cl. Acta Zoologica Fennica 24:1–42.

Petrusewicz, K. 1938. Badania ekologiczne nad krzyżakami Argiopidae na the fizjografji wileńszczyzny. Prace Towarzystwa Przyjaciól Nauk W Wilnie 12:1–83.

Peus, F. 1928. Beiträge zur Kenntnis der Tierwelt nordwestdeutscher Hochmoore. Eine ökologische Studie. Insekten, Spinnentiere teilw. Wirbeltiere. Zeitschrift Morphologie und Ökologie Tiere 12:531–683.

Platnick, N.I. 2005. The world spider catalog, version 6.0. American Museum of Natural History, online at http://research.amnh.org/entomology/spiders/catalog81-87/index.html

Platt, J.R. 1964. Strong inference. Science 146:347–353.

Pointing, P.J. 1965. Some factors influencing the orientation of the spider, *Frontinella communis* (Hentz.), in its web (Araneae:Linyphiidae). Canadian Entomologist 97:69–78.

Popper, K.R. 1977. The Logic of Scientific Discovery. Routledge, London

Quammen, D. 1996. Song of the Dodo. Plimlico, London.

Quinn, J.F. & A.E. Dunham. 1983. On hypothesis testing in ecology and evolution. American Naturalist 122:602–617.

Rau, P. 1922. Ecological and behavior notes on Missouri insects. Transactions of the Academy of Science of St. Louis 24:1–71.

Rau, P. 1926. The ecology of a sheltered clay bank: a study in insect sociology. Transactions of the Academy of Science of St. Louis 25:157–277.

Richter, C.J.J. 1967. Aeronautic behaviour in the genus *Pardosa* (Araneae, Lycosidae). Entomologist's Monthly Magazine 103:72–74.

Richter, C.J.J. 1970a. Aerial dispersal in relation to habitat in eight wolf spider species (*Pardosa*, Araneae, Lycosidae). Oecologia 5:200–214.

Richter, C.J.J. 1970b. Relation between habitat structure and development of the glandulae ampullaceae in eight wolf spider species (*Pardosa*, Araneae, Lycosidae). Oecologia 5:185–199.

Richter, C.J.J. 1971. Some aspects of aerial dispersal in different populations of wolf spiders, with particular reference to *Pardosa amentata* (Araneae, Lycosidae). Miscellaneous Papers Landbouwhogeschool Hogeschool, Wageningen, Netherlands 8:77–88.

Richter, C.J.J., J. Denholla & L. Vlijm. 1971. Differences in breeding and mortality between *Pardosa pullata* (Clerck) and *Pardosa prativaga* (L. Koch), (Lycosidae, Araneae) in relation to habitat. Oecologia 6:318–327.

Ricklefs, R.E. & G.L. Miller. 1999. Ecology. W.H. Freeman & Company, New York.

Riechert, S., W.G. Reeder & T.A. Allen. 1973. Patterns of spider distribution (*Ageleopsis aperta*) Gertsch)) in desert grassland and recent lava bed habitats, South-Central New Mexico. Journal of Animal Ecology 42:19–35.

Riechert, S.E. & C.R. Tracey. 1975. Thermal balance and prey availability: basis for a model relating web-site characteristics to spider reproductive success. Ecology 56:265–284.

Robinson, M.H. & B.C. Robinson. 1973. Ecology and behavior of the giant wood spider *Nephila maculata* (Fabr.) in New Guinea. Smithsonian Contributions to Zoology 149:1–76.

Schaefer, M. 1972. Ökologische Isolation und die Bedeutung des Konkurrenzfaktors am Beispiel des Verteilungsmusters der Lycosiden einer Küstenlandschaft. Oecologia 9:171–202.

Shelford, V.E. 1912. Ecological succession. IV. Vegetation and the control of land animal communities. Biological Bulletin of the Marine Biological Laboratory 23:59–99.

Shelford, V.E. 1930. Ways and means of improving the quality of investigation and publication in animal ecology. Ecology 11:235–237.

Shulov, A. 1940. On the biology of two *Latrodectus* spiders in Palestine. Proceedings of the Linnean Society, London 152:309–328.

Simberloff, D.S. & E.O. Wilson. 1969. Experimental zoogeography of islands: the colonisation of empty islands. Ecology 50:278–296.

Simon, E. 1892. Histoire naturelle des araignées. Paris 1:1–256.

Simon, E. 1893. Histoire naturelle des araignées. Paris 1:257–488.

Simon, E. 1894. Histoire naturelle des araignées. Paris 1:489–760.

Simon, E. 1895. Histoire naturelle des araignées. Paris 1:761–1084.

Simon, E. 1897. Histoire naturelle des araignées. Paris 2:1–192.

Simon, E. 1898. Histoire naturelle des araignées. Paris 2:193–380.

Simon, E. 1901. Histoire naturelle des araignées. Paris 2:381–668.

Simon, E. 1903. Histoire naturelle des araignées. Paris 2:669–1080.

Southwood, T.R.E. 1977. Habitat, the templet for ecological strategies. Journal of Animal Ecology 46:337–365.

Statzner, B., A.G. Hildrew & V.H. Resh. 2001. Spe-

cies traits and environmental constraints: entomological research and the history of ecological theory. Annual Reviews of Entomology 46:291–316.

Sudd, J.H. 1972. Distribution of spiders at Spurn Head (E. Yorkshire) in relation to flooding. Journal of Animal Ecology 41:63–70.

Suter, R.B. 1981. Behavioral thermoregulation: solar orientation in *Frontinella communis* (Linyphiidae), a 6-mg spider. Behavioral Ecology and Sociobiology 8:77–81.

Toft, S. 2002. Edwin Nørgaard. Pp. 13–16. *In* European Arachnology 2000. (S. Toft & N. Scharff eds). Arhus, Denmark.

Tretzel, E. 1952. Zur Ökologie der spinnen Araneae. Autokologie der arten en raum von erlangen. Sitzungsberichten der Physikalisch-Medizinishen Sözietat in Erlangen 75:36–113.

Tretzel, E. 1954. Reife-und Fortpflanzungszeit bei Spinnen. Zeitschrift Morphologie und Ökologie Tiere 42:634–691.

Tretzel, E. 1955. Intragenerische isolation und interspezifische konkurrenz bei spinnen. Zeitschrift Morphologie und Ökologie Tiere 44:43–162.

Turchin, P. 1999. Population regulation: a synthetic view. Oikos 84:153–159.

Turchin, P. 2001. Does population ecology have general laws? Oikos 94:17–26.

Turnbull, A.L. 1960. The spider population of a stand of oak (*Quercus robur* L.) in Wytham Wood, Berks., England. Canadian Entomologist 92:110–124.

Turnbull, A.L. 1973. Ecology of the true spiders (Araneomorphae). Annual Reviews of Entomology 18:305–348.

Van Hook, R.I.,Jr. 1971. Energy and nutrient dynamics of spider and orthopteran populations in a grassland ecosystem. Ecological Monographs 41:1–26.

Varley, G.C. 1947. The natural control of population balance in the knapweed gall-fly (*Urophora jaceana*). Journal of Animal Ecology 16:139–187.

Varley, G.C., G.R. Gradwell & M.P. Hassell. 1973. Insect Population Ecology. An analytical approach. Blackwell Scientific Publications, Oxford.

Vlijm, L., A. Kessler & C.J.J. Richter. 1963. The life history of *Pardosa amentata* (Cl.) (Araneae: Lycosidae). Entomologische Berichten, Amsterdam 23:75–80.

Vlijm, L. & A.M. Kessler-Geschiere. 1967. The phenology and habitat of *Pardosa monticola*, *P. nigriceps* and *P. pullata* (Araneae:Lycosidae). Journal of Animal Ecology 36:31–56.

Volterra, V. 1926. Variazioni e fluttuazioni del numero d'individui in specie animali conviventi. Memorie dell'Accademia dei Lincei 6:31–113.

von Haartman, L. 1994. In memoriam: Pontus Palmgren, 1907–1993. The Auk 111:995–996.

Weese, A.O. 1924a. Animal ecology of an Illinois elm -maple forest. Illinois Biological Monographs 9:1–93

Weese, A.O. 1924b. Animal ecology of an Illinois elm -maple forest. Illinois Biological Monographs 9:345–438.

Wilson, E.O. & D. Simberloff. 1969. Experimental zoogeography of islands: defaunation and monitoring techniques. Ecology 50:267–278.

Wise, D. 1993. Spiders in Ecological Webs. Cambridge University Press, Cambridge.

Manuscript received 1 October 2005, revised 10 November 2005.

2005. The Journal of Arachnology 33:850–851

SHORT COMMUNICATION

FOOD STORAGE BY A WANDERING GROUND SPIDER (ARANEAE, AMMOXENIDAE, *AMMOXENUS*)

Ansie S. Dippenaar-Schoeman: ARC–Plant Protection Research Institute, Private Bag X134, Pretoria, 0001 South Africa

Rupert Harris: 99 Colonel Trichardt Street, Welgelegen, Pietersburg, 0699 South Africa

ABSTRACT. Members of genus *Ammoxenus* are known predators of harvester termites (*Hodotermes mossambicus*). An *A. amphalodes* female was observed catching and paralyzing a termite in the field. The paralyzed termite was deposited in a silk sac with other paralyzed termites. This confirms that *Ammoxenus* spp. use different methods of catching and utilizing prey. Termites are either killed and fed upon or paralyzed and stored for feeding at a later time.

Keywords: Termites, Africa feeding behavior

Ammoxenus Simon 1892 are known predators of the harvester termite, *Hodotermes mossambicus* (Hagen 1858) in southern Africa (Wilson & Clark 1977; Van den Berg & Dippenaar-Schoeman 1991; Dippenaar-Schoeman et al. 1996a, b). Harvester termites forage in sporadic bursts of activity on the soil surface from subterranean nests. When present in high numbers they can cause severe damage to grassland, especially during long periods of drought. Ammoxenid spiders are free-living soil-dwellers, also known as sand divers due to their ability to dive headfirst into sand when disturbed. *Ammoxenus* are known only from southern Africa, with six described species occurring throughout the region (Dippenaar & Meyer 1980). They are commonly found in high numbers in areas infested with harvester termites.

Ammoxenus are regarded as specialist predators of harvester termites (Dippenaar-Schoeman et al. 1996b). They are invariably found in the soft soil mounds left after excavation by the termites in close proximity to the nest entrance. They are able to detect termite foraging activity either through soil vibration or chemical cues. According to Dean (1988) the spiders use tactile cues to select optimal prey items after initial handling of the prey. During prey capture, the termite is grabbed and bitten between the head capsule and the cephalothorax. The dead termite is pulled below the soil surface by the spider before feeding commences. Prey is sucked out and not chewed. Van den Berg & Dippenaar-Schoeman (1991) observed that members of *Ammoxenus amphalodes* Dippenaar & Meyer 1988 spend inactive periods in sac-like retreats made in the soft soil humps left by the termites during excavations of their subterranean nests. Along with the retreat sacs, other soft silk sacs containing dead harvester termites (4–8 termites per sac) were collected from the soil mounds at Rietondale Research Station, Pretoria (25°14′S, 28° 15′E). Van den Berg & Dippenaar-Schoeman (1991) speculated that these termites might serve as a food reserve for the spiders during the long periods when the termites are inactive. The observations described here confirm this.

On 21 April 1998 an *A. amphalodes* female was observed in a grassy field near Pietersburg (23°54′S, 29°28′E) in the Limpopo Province of South Africa. She ran with great speed amongst workers of the harvester termite and then suddenly ran towards a termite worker, leaped onto it and delivered a bite to the side of the termite's body just above the base of the second leg. The spider flexed her legs backward while administering the bite. Within 30 sec the struggling termite slowed down. The spider released the termite for less than a sec to administer a second bite to one of the legs of the termite that lasted about 20 sec. The spider then dragged the still-living, but paralyzed, termite about 40 cm to a soft sandy area. She entered a soft sac-like structure on the soil surface that was well camouflaged with sand particles. The form of the sac, with its flap-like entrance, was similar to that of a sleeping bag lying flat on the soil surface. The spider used her front legs to open the sac and dragged the termite into the sac. Movement within the sac continued for about 5 min.

At this stage the sac with its contents was col-

lected along with the female spider. The sac contained four termites which appeared dead but, when touched, movement of their legs was observed. There was no indication that they had been fed upon. The sac was about 10 cm in diameter and the interior consisted of a white, slightly shiny smooth silk layer while the outside was slightly sticky and covered with sand particles. The spiders and termites are voucher specimens housed in the National Collection of Arachnida at the ARC-Plant Protection Research Institute in Pretoria.

Harvester termites have erratic bursts of activity. The ammoxenids are able to detect these bursts whether they occur nocturnally or diurnally (Wilson & Clark 1977; Dippenaar-Schoeman et al. 1996a, b). The termites are thus available sporadically, for short periods, above ground to the spiders. Web building spiders have been observed storing termite prey during at least short periods when food is abundant. The theridiid *Chrosiothes tonala* Levi 1954, which is also a termite specialist, could capture during a single burst of termite activity 20 prey or more before carrying them all off in one prey mass (Eberhard 1991). In the field these spiders were observed feeding on the prey mass for up to a day. The extra prey captured therefore enabled the spiders to feed over a longer period.

This observation of food storage strengthens the assumption that members of *Ammoxenus* are specialist predators of termites (Dippenaar- Schoeman et al. 1996b). They seem to use two different methods of catching and utilizing prey. The termite workers are either killed, pulled immediately below the soil surface and fed upon or they are paralyzed and stored in silk sacs just below the soil surface for feeding at a later stage.

LITERATURE CITED

Dean, W.R.J. 1988. Spider predation on termites (Hodotermitidae). Journal of the Entomological society of Southern Africa 51:147–148.

Dippenaar, A.S. & M.K.P. Meyer. 1980. On the species of the African genus*Ammoxenus* (Araneae: Ammoxenidae), with descriptions of two new species. Journal of the Entomological Society of Southern Africa 43:41–49.

Dippenaar-Schoeman, A.S., M. de Jager & A. van den Berg. 1996a. Behaviour and biology of two species of termite-eating spiders, *Ammoxenus amphalodes* and *A. pentheri* (Araneae: Ammoxenidae), in South Africa. African Plant Protection 2:15–17.

Dippenaar-Schoeman, A.S., M. de Jager & A. van den Berg. 1996b. *Ammoxenus* species (Araneae: Ammoxenidae) specialist predators of harvester termites in South Africa. African Plant Protection 2:103–109.

Eberhard, W.G. 1991. *Chrosiothes tonala* (Araneae, Theridiidae): A web-building spider specializing on termites. Psyche 98:7–19.

Van den Berg, A. & A.S. Dippenaar-Schoeman. 1991. Ground-living spiders from an area where the harvester termite *Hodotermes mossambicus* occurs in South Africa. Phytophylactica 23:247–253.

Wilson, D.S. & A.B. Clark. 1977. Above ground predator defense in the harvester termite, *Hodotermes mossambicus*(Hagen). Journal of the Entomological Society of Southern Africa 40:271–282.

Manuscript received 1 June 2000, revised 5 January 2005.

2004. The Journal of Arachnology 32:852–856

SHORT COMMUNICATION

PARTHENOGENESIS THROUGH FIVE GENERATIONS IN THE SCORPION *LIOCHELES AUSTRALASIAE* (FABRICIUS 1775) (SCORPIONES, ISCHNURIDAE)

Kazunori Yamazaki[1]: Institute of Life and Environmental Sciences, University of Tsukuba, Tsukuba, Ibaraki 305-8572, Japan

Toshiki Makioka[2]: Institute of Biological Sciences, University of Tsukuba, Tsukuba, Ibaraki 305-8572, Japan

ABSTRACT. Females of *Liocheles australasiae* (Fabricius 1775) collected from a maleless population on Iriomote Island, Ryukyu, Japan, and separately reared in the laboratory have parthenogenetically produced five successive generations in seven years. Many individuals of the first generation collected in July 1994, gave birth to the second generations from 1994–1998, and some of the second generation gave birth to the third generation from 1997–1999. The fourth generations were born from 1999–2001, and the fifth generations were born in January–August 2001. Most females of all generations gave birth to about 20 neonates after approximately an eight-month pregnancy. In the ovary of a fourth generation female, as well as in those of most of the second generation females, there were growing embryos and a number of oocytes of various sizes, suggesting a possibility of the sixth generation or subsequent generations by parthenogenesis.

Keywords: Thelytokous parthenogenesis, successive generations, histological section

Among 1259 scorpion species described in the world (Fet et al. 2000), thelytokous parthenogenesis has been reported only in seven species (Matthiesen 1962, 1971; San Martín & Gambardella 1966; Makioka & Koike 1984, 1985; Zolessi 1985; Lourenço 1991; Lourenço & Cuellar 1994; Makioka 1993; Maury 1997; Lourenço et al. 2000). In some of these species, parthenogenesis has been presumed based on the absence of males in the populations (Lourenço 1991; Lourenço & Cuellar 1994), female biased sex ratios (Maury 1997) and all female neonates (Lourenço 1991; Lourenço & Cuellar 1999). However, one of the best evidences of parthenogenesis is an achievement of independent rearing, i.e., being raised alone without the presence of males, through successive generations. In only three scorpion species, has parthenogenesis been confirmed by means of independent rearing through three or four successive generations; this was seen in two buthids, *Tityus serrulatus* Lutz & Mello 1922 (Matthiesen 1962, 1971; San Martín & Gambardella 1966) and *T. bolivianus uruguayensis* (Borelli 1900) (Zolessi 1985) and an ischnurid, *Liocheles australasiae* (Fabricius 1775) (Makioka 1993).

Matthiesen (1962) found in *Tityus serrulatus* that three individuals of the second generation, born from the first field-collected generation, parthenogenetically gave birth to the third generations when reared separately. Later he reported that one of the third generation individuals, reared separately, gave birth to a total of 33 fourth generation offspring (Matthiesen 1971). In *T. serrulatus*, San Martín & Gambardella (1966) also reported that two second generation females gave birth to 22 third generation offspring, only two of which gave birth to eight fourth generation offspring. Zolessi (1985) stated that, for *T. bolivianus uruguayensis* he successively obtained second and third generations when females were reared separately, but he did not show the numbers of mothers and neonates. In *Liocheles australasiae* Makioka (1993) obtained many third generation offspring under separate rearing conditions. In these previous works, however, only a few of the second or third generations produced offspring particularly in the *Tityus* species, and no neonates of the third or the fourth generations became mature to produce offspring, leaving unanswered the ques-

[1] Present address: Department of Biological Sciences, Graduate School of Science, University of Tokyo, 7-3-1 Hongo, Bunkyo-ku, Tokyo, 113-0033, Japan.

[2] Present address: 4-31-13 Kitami, Setagaya, Tokyo 157-0067, Japan.

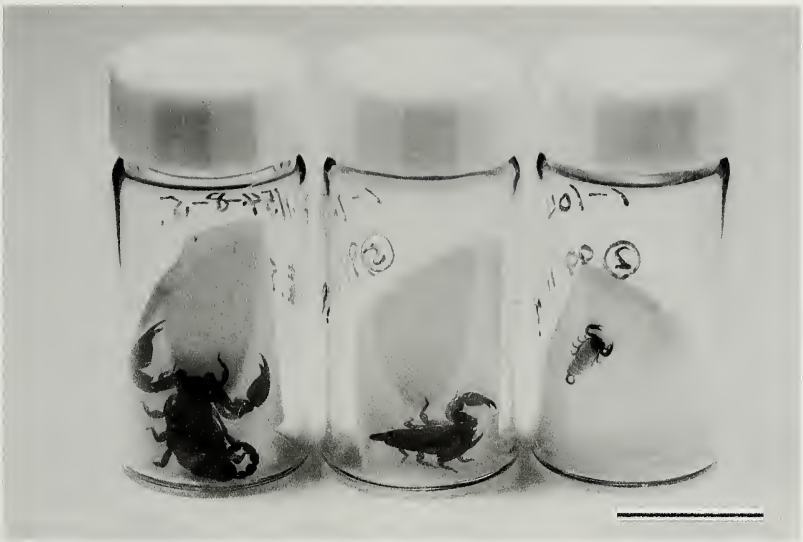


Figure 1.—Separate rearing in *Liocheles australasiae*. Scale = 2 cm.

tion as to whether parthenogenesis is an evolutionary strategy in these species or whether the phenomenon is limited to only a few generations. In the present study, we have attempted to answer this question in *L. australasiae* by rearing them through more than four generations.

A total of 413 females of *Liocheles australasiae* were collected from a maleless population (Makioka & Koike 1984, 1985; Makioka 1992a, 1992b, 1993) on Iriomote Island, one of the Ryukyu Islands, Japan, in July 1994. These specimens are deposited in the collections of the Biological Sciences of University of Tsukuba (TKB-anim. 1008–1421). First generations derived from the collected specimens were serially numbered and kept separate in glass vials (27 mm in diameter and 55 mm in height) with a piece of wet filter paper (Fig. 1) at 28 ± 1 °C in a dark incubator, and fed termites once a week.

The first instar juveniles of the second generation born from those females immediately climbed onto their mother's back, stayed there without eating for about a week (Fig. 2), and then molted into second instar juveniles (Fig. 3) which left their mother and took food by themselves. Each of the second instar juveniles was kept separate in a new glass vial soon after the first molt, and serially numbered. The juveniles were fed termites once a week, the number of which was varied with the scorpion's instar. We took special care not to give soldier termites to the young scorpions, because the soldiers can wound or kill young scorpions. All specimens were watered daily and their conditions (molt, parturition, death, etc.) were checked and recorded.

Ten females of the second generation that experienced parturitions at least once and a female of the fourth generation that experienced parturition once were dissected in physiological saline solution for histological observations. The ovaries were removed, fixed with Bouin's solution, dehydrated in a graded ethanol-*n*-butanol series, embedded in paraffin and serially sectioned at 5 μm thickness. The sections were stained with Mayer's hematoxylin and eosin, and the number of oocytes, embryos growing in the ovarian diverticula, and empty ovarian diverticula (remnants of previous parturitions) was counted under a light microscope.

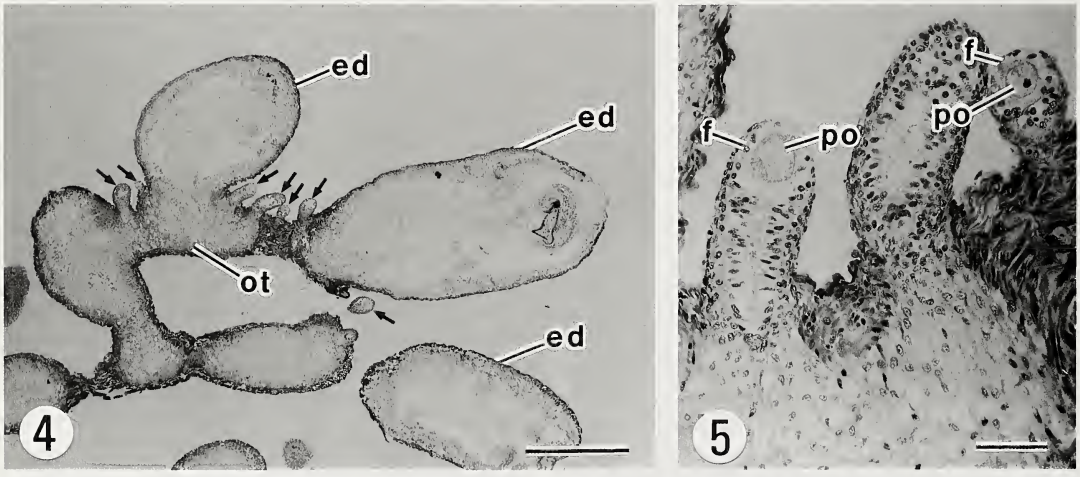
A total of 147 of the 413 first-generation females experienced 165 parturitions to produce 1118 second generation offspring during the period from 1994–1998. From these second generation offspring, 46 females became mature and experienced 98 parturitions to produce 493 third generation offspring, 19 of which experienced 28 parturitions to produce 180 fourth generation offspring. From the fourth generations, only seven females became mature and gave birth to 78 fifth generation offspring through six parturitions.

The ovary of each female dissected consisted of three longitudinal and four transverse ovarian tubes, which bore many growing ovarian diverticula containing oocytes or embryos and empty ovarian diverticula which had lost their embryos in the previous parturitions. In adult ovaries, as described in previous papers (Makioka 1992a; Yamazaki & Makioka 2001), there were neither oogonia nor oocytes in the walls of the ovarian tubes and all the oocytes were contained in their own ovarian diverticula, waiting to develop into embryos.

In the ovary of the fourth generation female examined immediately after her death, there were 20 large empty ovarian diverticula that had newly lost

Figure 2–3.—First instar juveniles of *Liocheles australasiae* mounted on their mother's back. Scale = 1 cm. 3. Second instar juveniles of *Liocheles australasiae* immediately after the first molt on their mother's back. Scale = 1 cm.

their embryos at the last parturition (Fig. 4) and 86 smaller ovarian diverticula containing oocytes of various sizes (Fig. 5). No growing ovarian diverticula containing growing embryos were found. Two neonates corresponding to the difference in number between 20 empty ovarian diverticula and 18 neonates counted at birth, may have been eaten by the mother (see Polis & Sissom 1990). Neither male gonadal tissues, such as ovotestes, nor sperm receiving structures, such as spermathecae, were



Figures 4–5.—Ovarian sections of the fourth generation in *Liocheles australasiae*. 4. Ovarian diverticula containing a primary oocyte (arrows) and empty ovarian diverticula (ed). ot, ovarian tube. Scale: 500 μm. 5. Enlargement of small ovarian diverticula containing primary oocyte (po). f; follicle epithelium. Scale = 50 μm.

found in the ovaries of the second and the fourth generation females.

Some authors have attempted to rear scorpions from neonates to adults in order to ascertain their life histories (Rosin & Shulov 1963; Smith 1966; Matthiesen 1970; Francke 1976; Sissom & Francke 1983; Francke & Sissom 1984; Benton 1991; Brown 1997) and to confirm parthenogenetic reproduction (Matthiesen 1962, 1971; San Martín & Gambardella 1966; Zolessi 1985; Makioka 1993; Lourenço & Cuellar 1999). In most cases, however, none or only a few of neonates reached the adult stage (Matthiesen 1962, 1970, 1971; Rosin & Shulov 1963; San Martín & Gambardella 1966; Smith 1966; Francke 1976; Sissom & Francke 1983; France & Sissom 1984; Zolessi 1985; Benton 1991; Brown 1997). Among them, only three parthenogenetic scorpions successively continued to produce subsequent generations under the separate rearing conditions (Matthiesen 1962, 1971; San Martín & Gambardella 1966; Zolessi 1985; Makioka 1993).

Matthiesen (1971) succeeded in obtaining 33 neonates of the fourth generation from a mother of the third generation in *Tityus serrulatus* and Zolessi (1985) obtained an unspecified number of neonates of the third generation from the second generation in *T. bolivianus uruguayensis*, but they did not mention the fates of these neonates. In *Liocheles australasiae*, Makioka (1993) obtained a number of neonates of the third generation from four mothers of the second generation, but rearing was then terminated by an incubator accident. Thereafter, in 1994, we began the present study and have succeeded in obtaining a number of individuals of five successive generations of *L. australasiae*. At present, 78 second instars of the fifth generation are being raised. At the same time, in a fourth generation female after the first parturition, the ovary contained a number of oocytes of various sizes. It seems likely therefore, that the present specimens of *L. australasiae* will continue to reproduce parthenogenetically through further generations under the present laboratory conditions, as well as in their native population of Iriomote Island, and that our separate rearing method is well suited to *L. australasiae*. We suggest that because of the number of offspring produced by parthenogenesis and because of the number of generations we have now reared, parthenogenesis is indeed a stable reproductive strategy in this species.

We wish to thank Dr. Koji Tojo, University of Tsukuba, for his helpful advice on preparing the present paper. We also thank Dr. Hiroshi Ando, Tsurumi University, and Mr. Yuji Takayama and Mr. Hiroyuki Mitsumoto, University of Tsukuba, for their assistance in collecting and rearing specimens.

LITERATURE CITED

Benton, T.G. 1991. The life history of *Euscorpius flavicaudis* (Scorpiones, Chactidae). Journal of Arachnology 19:105–110.

Brown, C.A. 1997. Growth rates in the scorpion *Pseudouroctonus reddelli* (Scorpionida, Vaejovidae). Journal of Arachnology 25:288–294.

Fet, V., Sissom, W.D., Lowe, G. & Braunwalder, M.E. 2000. Catalog of the Scorpions of the World (1758–1998). New York Entomological Society, New York, 690 p.

Francke, O.F. 1976. Observations on the life history of *Uroctonus mordax* Thorell (Scorpionida, Vaejovidae). Bulletin of the British Arachnologigal Society 3:254–260.

Francke, O.F. & Sissom, W.D. 1984. Comparative review of the methods used to determine the number of molts to maturity in scorpions (Arachnida), with analysis of the post-birth development of *Vaejovis coahuilae* Williams (Vaejovidae). Journal of Arachnology 12:1–20.

Lourenço, W.R. 1991. Parthenogenesis in the scorpion *Tityus columbianus* (Thorell) (Scorpiones: Buthidae). Bulletin of the British Arachnological Society 8:274–276.

Lourenço, W.R. & Cuellar, O. 1994. Notes on the geography of parthenogenetic scorpions. Biogeographica 70:19–23.

Lourenço, W.R. & Cuellar, O. 1999. A new all-female scorpion and the first probable case of arrhenotoky in scorpions. Journal of Arachnology 27:149–153.

Lourenço, W.R., Cloudsley-Thompson, J.L. & Cuellar, O. 2000. A review of parthenogenesis in scorpions with a description of postembryonic development in *Tityus metuendus* (Scorpiones, Buthidae) from western amazomia. Zoologischer anzeiger 239:267–276.

Makioka, T. 1992a. Reproductive biology of the viviparous scorpion, *Liocheles australasiae* (Fabricius) (Arachnida, Scorpiones, Ischnuridae). II. Repeated pregnancies in virgins. Invertebrate Reproduction and Development 21:161–166.

Makioka, T. 1992b. Reproductive biology of the viviparous scorpion, *Liocheles australasiae* (Fabricius) (Arachnida, Scorpiones, Ischnuridae). III. Structural types and functional phases of the adult ovary. Invertebrate Reproduction and Development 21:207–214.

Makioka, T. 1993. Reproductive biology of the viviparous scorpion, *Liocheles australasiae* (Fabricius) (Arachnida, Scorpiones, Ischnuridae). IV. Pregnancy in females isolated from infancy, with notes on juvenile stage duration. Invertebrate Reproduction and Development 24:207–212.

Makioka, T. & Koike, K. 1984. Parthenogenesis in the viviparous scorpion, *Liocheles australasiae*. Proceedings of the Japan Academy 60, series B, No. 9:374–376.

Makioka, T. & Koike, K. 1985. Reproductive biology of the viviparous scorpion, *Liocheles australasiae* (Fabricius) (Arachnida, Scorpiones, Scorpionidae). I. Absence of males in two natu-

ral populations. International Journal of Invertebrate Reproduction and Development 8:317–323.

Matthiesen, F.A. 1962. Parthenogenesis in scorpions. Evolution 16:255–256.

Matthiesen, F.A. 1970. Le développement post-embryonnaire du scorpion Buthidae: *Tityus bahiensis* (Perty, 1834). Bulletin du Muséum National d'Histoire Naturelle, Paris 41:1367–1370.

Matthiesen, F.A. 1971. The breeding of *Tityus serrulatus* Lutz & Mello, 1927, in captivity (Scorpions, Buthidae). Revista rasileira de pesquisas médicas e Biológicas 4:299–300.

Maury, E.A. 1997. *Tityus trivittatus* en la Argentina. Nuevos datos sobre distribución, partheno-genesis, sinantropia y peligrosidad (Scorpiones, Buthidae). Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" 24: 1–24.

Polis, G.A. & Sissom, W.D. 1990. Life history. Pp. 161–223. *In* Biology of Scorpions. (G.A. Polis, ed.). Stanford University Press, Stanford, California.

Rosin, R. & Shulov, A. 1963. Studies on the scorpion *Nebo hierochonticus*. Proceedings of Zoological Society of London 140:547–575.

San Martín, P.R. & De Gambardella, L. A. 1966. Nueva comprobacion de la partenogenesis en *Tityus serrulatus* Lutz y Mello-Campos 1922 (Scorpionida, Buthidae). Revista de la Sociedad de Entomología de Argentina 28:79–84.

Sissom, W.D. & Francke, O.F. 1983. Post-birth development of *Vaejovis bilineatus* Pocock (Scorpiones: Vaejovidae). Journal of Arachnology 11: 69–75.

Smith, G.T. 1966. Observations on the life history of the scorpion *Urodacus abruptus* Pocock (Scorpionidae), and an analysis of its home sites. Australian Journal of Zoology, 14:383–398.

Yamazaki, K. & Makioka, T. 2001. Ovarian structural features reflecting repeated pregnancies and parturitions in a viviparous scorpion, *Liocheles australasiae*. Zoological Science, 18:277–282.

Zolessi, L.C. 1985. La partenogenesis en el escorpion amarillo *Tityus bolivianus uruguayensis* (Borelli, 1900) (Scorpionida: Buthidae). Actas de las Jornadas de Zoologia del Uruguay 13–14.

Manuscript received 18 March 2002, revised 22 October 2003.

2005. The Journal of Arachnology 33:857–861

SHORT COMMUNICATION

THE EFFECTS OF MOISTURE AND HEAT ON THE EFFICACY OF CHEMICAL CUES USED IN PREDATOR DETECTION BY THE WOLF SPIDER *PARDOSA MILVINA* (ARANEAE, LYCOSIDAE)

Shawn M. Wilder and **Jill DeVito**: Department of Zoology, Miami University, Oxford, OH 45056

Matthew H. Persons: Department of Biology, Susquehanna University, Selinsgrove, PA 17870

Ann L. Rypstra: Department of Zoology, Miami University, Hamilton, OH 45011

ABSTRACT. Little is known about how environmental conditions affect the relative efficacy of information present in chemical cues. The wolf spider, *Pardosa milvina*, responds to silk and excreta from a larger species of wolf spider, *Hogna helluo*, with effective antipredator behavior. We investigated whether wetting or heating chemotactile cues of *Hogna helluo* would reduce the amount of antipredator behavior displayed by *Pardosa milvina* relative to unmanipulated cues. *Pardosa milvina* showed less antipredator behavior on chemotactile cues that had been wetted then dried but did not respond differently in the presence of cues that had been heated and then cooled. The results suggest that, in the field, morning dew may degrade some of the cues deposited by *H. helluo* at night and reduce the ability of *P. milvina* to avoid predation. However, typical periods of daily heating of cues may not affect the efficacy of predator detection by *P. milvina*.

Keywords: Antipredator behavior, chemotactile cues, moisture, heat

Many animals have evolved behaviors that reduce the risk of predation, often at the cost of lost foraging opportunities (Sih 1980; Stephens & Krebs 1986). To minimize the costs of antipredator behavior, some animals adjust their behavioral response to a predator depending on the relative magnitude of the threat (Kats & Dill 1998; Dicke & Grostal 2001). A variety of cues, including visual information, vibrations, and chemicals, may be used to detect the presence of and threat posed by a predator (Lima & Dill 1990). Chemotactile cues may be especially important for predator detection by the wolf spider *Pardosa milvina* (Hentz 1844) (Araneae, Lycosidae; Persons et al. 2002). This relatively small wolf spider (ca. 20 mg) significantly reduces movement in the presence of silk and excreta from the larger (adult female, ca. 300–800 mg) syntopic wolf spider *Hogna helluo* (Walckenaer 1837) (Araneae, Lycosidae; Persons & Rypstra 2001; Barnes et al. 2002). This reduction in movement results in a lower probability of predation for *P. milvina* (Persons et al. 2002). However, long term exposure to cues can have significant costs, including weight loss and lower egg production (Persons et al. 2002). Thus, *P. milvina* finely adjusts its antipredator behavior depending on the size of the predator (Persons & Rypstra 2001), the diet of the predator (Persons et al. 2001), and the length of time since predator cues were deposited (Barnes et al. 2002).

The level of antipredator behaviors exhibited (i.e. reductions in activity) may depend on the reliability of cues present in the environment. Past studies of the response of *P. milvina* to cues of *H. helluo* have been conducted in controlled laboratory environments (Barnes et al. 2002; Persons et al. 2002). Yet, in nature, cues may be exposed to a variety of environmental conditions that may affect the quality of cues and the information they contain about a predator. Even within a single day, conditions may change from cool and wet (e.g. from dew) in the morning, to hot and dry during the middle of the day. Information is needed on how environmental conditions may affect predator cues in order to extrapolate the results of laboratory studies to the natural environment. The purpose of the study was to

examine the impact of two potentially important environmental variables, moisture and heat, on the relative efficacy of chemotactile cues that induce antipredator behavior by *P. milvina*.

All *P. milvina* used as experimental subjects were collected in the soybean fields at the Miami University Ecology Research Center (Oxford, Butler County, Ohio, USA) between June and August 2003. We used field caught adult female *P. milvina* in the experimental trials. None of the females used in the trials had produced an egg sac in the week prior to testing. *Hogna helluo* used for cue collection were adult and late instar immature females, all of which had been either field-caught or lab-reared from populations originating at the Ecology Research Center.

Both species were maintained in covered plastic cups (*P. milvina*: 5 cm high × 8 cm wide, *H. helluo*: 8 cm high × 12 cm wide) with a moist peat moss substrate in the laboratory on a 13:11 light: dark cycle at approximately 25 °C and 70% humidity. Both *P. milvina* and *H. helluo* were maintained on a diet of two appropriately sized domestic cricket nymphs (*Acheta domesticus*) once a week. The predators to be used as a source of chemotactile stimuli, *H. helluo*, were fed to satiation with eight juvenile crickets in the 24 hours preceding cue collection. This served to equalize the potential volume of silk and feces deposited on the substrate.

We collected predator silk and excreta cues on white filter paper (18.5 cm diameter) housed in covered, round plastic containers (20 cm in diameter × 8 cm high). Chambers were swabbed with alcohol and allowed to dry before we added the filter paper. A cotton dental wick saturated with double-distilled water was taped to the inside of each container lid to prevent spider desiccation. A single *H. helluo* was housed in each chamber for a minimum of 24 h (i.e., preceding the first trial run on a given day). Because the level of *P. milvina* response to *H. helluo* cues declines with cue age (Barnes et al. 2002), we did not remove the stimulus spider from the cue collection chamber until we were ready to treat the cue-laden filter paper with water or heat two hours before each trial.

The testing arena consisted of the same container type used for cue collection, except that the lid was removed to allow video recording of each trial from above. For each trial, we lined one side of the arena with unmanipulated *H. helluo* cues (control) and the other side with *H. helluo* cues that had been exposed to one of our experimental treatments. Before handling filter paper, and between handling filter paper with unmanipulated cues and experimentally-manipulated cues, we cleaned our hands by washing them with soap and water and then sterilizing them with alcohol. Experimental vs. control sides were alternated between trials during each experiment (i.e., the left side of the arena was designated as the control in approximately 50% of the trials and vice versa). Arenas were swabbed with alcohol and allowed to dry between trials. Individual *P. milvina* were introduced to the center of the test chamber under a clear glass vial (2.5 cm in diameter × 6.5 cm high) on a small round circle of filter paper (diameter = 4.5 cm) which had not been exposed to predator cues. After an acclimation period of two minutes, we removed the glass vial and recorded *P. milvina* behavior remotely using a video camera.

We conducted trials from 25 August–5 September 2003, between 0930 h and 1630 h. The behavior of *P. milvina* was recorded from another room to minimize human disturbance during the trials. The video camera was mounted 1 m above the test chamber and the area was illuminated with fluorescent lighting; room temperature was ca. 25 °C. We quantified locomotor activity of the experimental *P. milvina* using an automated digital data collection system (Videomex-V, Columbus Instruments) connected to a Sony© Hi8 video camera. The system recorded spider movements on each side of the arena for one-minute intervals throughout each 30 min trial. We compared the following parameters between treatment and control sides of the arenas: distance traveled, time spent resting, time walking, residence time on each side of the arena, and time spent in non-forward movement (e.g. leg movements or turning). We discarded data from several animals that failed to move more than 100 cm during the 30 minute trial because these individuals may not have had sufficient experience sampling both sides of the arena. Typical distances traveled by *P. milvina* for 30 min in equivalent test arenas range from 300–1000 cm (Persons et al. 2001). We summed data over the 30 min trial and used paired t-tests to compare movement behaviors on the cue and control sides of the arena.

In our first experiment, *P. milvina* were given a choice between filter paper with *H. helluo* cues that had been saturated with water then allowed to dry for two hours (experimental treatment) vs. filter paper with cues collected from the same spider, not treated with water but allowed to age for the same two hour period (control treatment). Two hours before each trial, we removed the stimulus spider from the cue collection chamber, cut the filter paper in half with scissors, and wet the experimental section with 1.5 mL double-distilled water, dripped evenly across the cue-laden surface. Both experimental and control treatments (n = 14) were left open to the air (at room temperature ca. 22.5 °C; humidity ca. 60%) to allow the wet side to dry for 2 hours.

Our second experiment consisted of a choice test between *H. helluo* cue-laden filter paper that had been heated to 40 °C, then cooled to room temperature (experimental treatment) vs. filter paper with cues collected from the same spider, not heated but

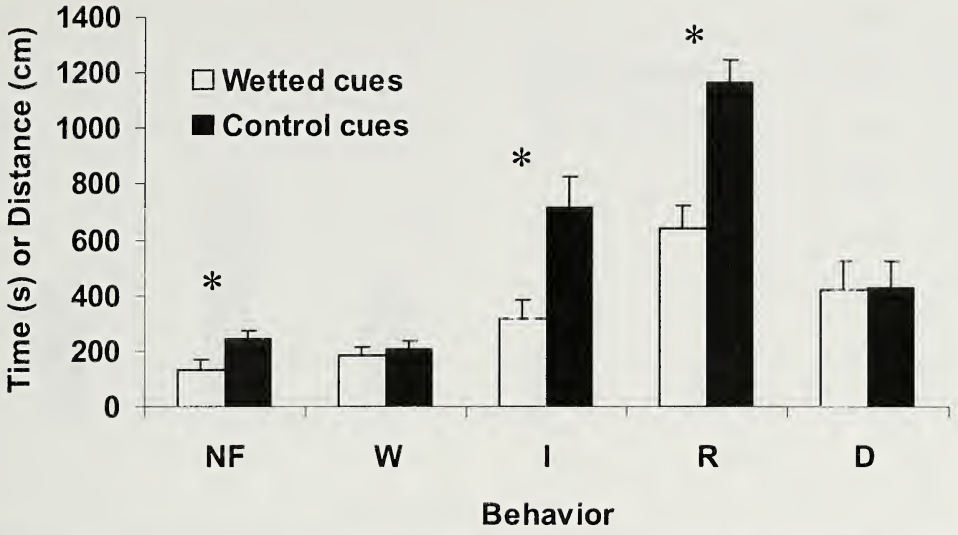


Figure 1.—Comparisons of the behavior of *P. milvina H. helluo* cues that were wetted then dried. Behaviors are denoted as follows: NF = time in non-forward movement, W = time walking, I = time immobile, R = residence time (on half of arena), D = Distance traveled. * indicates $P < 0.05$.

allowed to age for the same two hour period (control treatment). Mean daily soil surface temperatures range between 20 and 30 °C from June–August in corn and soybean fields, where *P. milvina* and *H. helluo* are found in high abundance (NSIDC 2002). Occasionally, temperatures may rise above 40 °C for brief periods. However, a temperature of 40 °C was chosen for this study to evaluate if typical periods of heating during the summer would be sufficient to degrade the information contained in H. helluo cues. We removed the stimulus *H. helluo* from each chamber and divided the filter paper; the experimental half was placed in a drying oven preheated to 40 °C for 1.5 h, while the control half aged at room temperature (ca. 22.5 °C; humidity ca. 60%). The experimental filter paper was kept covered during heating to minimize the effect of the drying oven on the water content of the cue-laden paper. Each control filter paper was kept covered while the corresponding paper in the experimental treatment was in the oven. Containers with both treatments were left open to the air at room temperature during the 30 minute cooling period.

Wetting then drying the predator cues had a significant effect on the movements of *P. milvina* (Fig. 1). Spiders spent less time in non-forward movement (e.g. turning and appendage movements) on the wetted side of the arena than the control side ($df = 8$, $t = 4.40$, $P = 0.002$, Fig. 1). In addition, *P. milvina* spent significantly less time immobile ($df = 8$, $t = 2.58$, $P = 0.03$) and had a lower residence time ($df = 8$, $t = 3.09$, $P = 0.02$) on the treatment side of the arena that had previously been wet (Fig. 1). There was no effect of wetting the cues on time spent walking ($df = 8$, $t = 1.37$, $P = 0.21$) or distance traveled ($df = 8$, $t = 0.23$, $P = 0.83$).

In contrast to the effects of water on cue efficacy, heating then cooling the predator cues had no effect on the movement of *P. milvina* (Fig. 2). There were no differences in non-forward movement ($df = 12$, $t = 1.55$, $P = 0.15$), time spent walking ($df = 12$, $t = 0.03$, $P = 0.98$), time immobile ($df = 12$, $t = 1.21$, $P = 0.25$), residence time ($df = 12$, $t = 1.36$, $P = 0.20$) and distance traveled ($df = 12$, $t = 0.79$, $P = 0.44$) of *P. milvina* between previously heated and control predator cues.

Previous studies have shown that *P. milvina* responds to *H. helluo* silk and excreta with greater time spent immobile and greater residence time on cue substrates relative to controls (Persons et al. 2001; Barnes et al. 2002). Immobility has been shown to be an effective means of reducing predation risk from *H. helluo*, which may hunt using visual and/or vibratory cues (Persons et al. 2002). Thus the increase in activity we observed on the side of the arena that had been treated with water suggests that the cues deposited by *H. helluo* are significantly less effective in producing anti-predator behavior in *P. milvina*. Likewise, the greater amount of time that the spiders spent immobile on the control side of the arena where there were more effective chemical cues likely resulted in the counterintuitive observation they actually had longer residence times on the side of the arena where they perceived greater risk. We suspect that the greater time spent in non-forward movement (e.g. turning and appendage movements) in the presence of cues may constitute directional sampling of predator

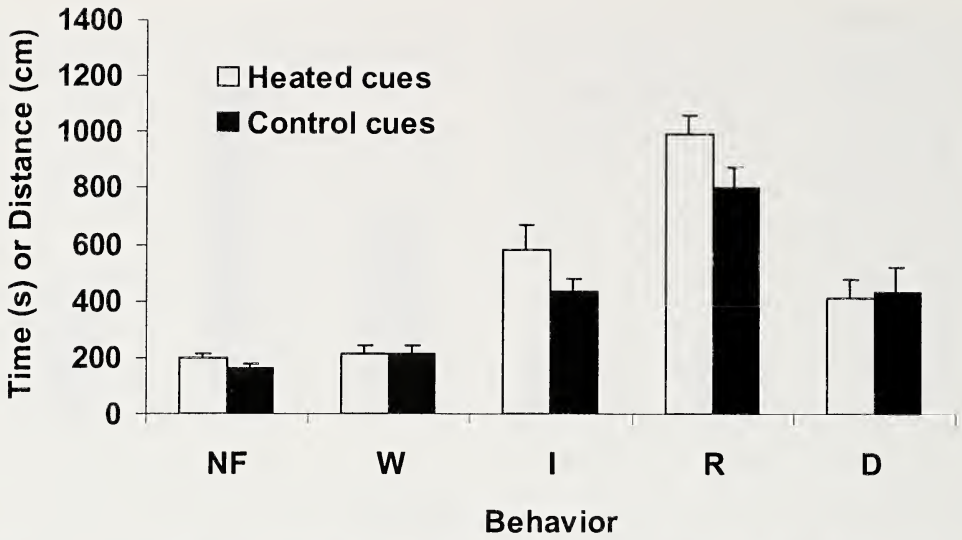


Figure 2.—Comparisons of behavior of *P. milvina* on *H. helluo* cues that were heated then cooled. Behaviors are denoted as follows: NF = time in non-forward movement, W = time walking, I = time immobile, R = residence time (on half of arena), D = Distance traveled.

cues and visual searching for nearby predators. Thus, less time in non-forward movement and less time immobile, and lower residence time on the previously wet substrate relative to control *H. helluo* cues, may indicate that water either reduces or completely eliminates the efficacy of the chemical cues used in predator detection by *P. milvina*.

The effects of water on predator cue efficacy may have important implications for *P. milvina*. *Hogna helluo* are primarily nocturnal and may deposit dense accumulations of silk and excreta around the entrance to their burrows, where they spend much of their time during the day (Walker et al. 1999a; b). Morning dew may then degrade much of the cues that were deposited at night and limit the ability of diurnal *P. milvina* to avoid or reduce movement in the proximity of *H. helluo* burrows. Periods after brief rainfall may also be dangerous to *P. milvina*. In addition to degrading predator cues, there is evidence that water degrades female sex pheromones, which may decrease the ability of males to find and mate with females (Dondale & Hegdekar 1973). Thus, the frequency of rainfall in a region may have implications for predator-prey interactions among *P. milvina* and *H. helluo*.

A temperature of 40 °C appeared to have no effect on the efficacy of *H. helluo* chemical cues. Lack of an effect of heating may be because the chemical cues in silk and excreta are tolerant of high temperatures, or because the heating period of the experiment was too short or of too low of a temperature to create a detectable difference. Further studies are needed to determine if longer periods of heating or higher temperatures, such as those experienced on some sunny summer afternoons on barren ground, where cues may be exposed to short periods (ca. 1–2 hours) of temperatures in excess of 40 °C, affect the efficacy of *H. helluo* chemical cues.

It is not known what chemical, group of chemicals or tactile information in the silk or excreta of *H. helluo* is responsible for eliciting antipredator behaviors in *P. milvina*. However, the results of this study suggest that the cue responsible for changes in behavior by *P. milvina* may degrade in the presence of water. Further studies of the properties of predator cues may aid in identifying the specific cue responsible for eliciting antipredator behavior in *H. helluo* silk and excreta.

ACKNOWLEDGMENTS

This manuscript was improved by comments from J. Rovner and an anonymous reviewer. We would like to thank the many undergraduates in the Miami University Spider Lab for collecting, raising and maintaining the spiders used in this study. Funding was provided by NSF grants DBI 0216776 & DBI 0216947 to M.H. Persons and A.L. Rypstra, an Ohio Plant Biotechnology Consortium grant to C.M. Buddle and A.L. Rypstra, and the Ecology Research Center and Department of Zoology at Miami University. Voucher specimens of *P. milvina* and *H. helluo* from the population at the Miami University Ecology Research Center have been deposited in Miami University's Hefner Zoology Museum.

LITERATURE CITED

Barnes, M.C., M.H. Persons & A.L. Rypstra. 2002. The effect of predator chemical cue age on an-

tipredator behavior in the wolf spider *Pardosa milvina* (Araneae: Lycosidae). Journal of Insect Behavior 15:269–281.

Dicke, M. & P. Grostal. 2001. Chemical detection of natural enemies by arthropods: an ecological perspective. Annual Review of Ecology and Systematics 32:1–23.

Dondale, C.D. & B.M. Hegdekar. 1973. The contact sex pheromone of *Pardosa lapidicina* Emerton (Araneida: Lycosidae). Canadian Journal of Zoology 51:400–401.

Kats, L.B. & L.M. Dill. 1998. The scent of death: chemosensory assessment of predation risk by prey animals. Ecoscience 5:361–394.

Lima, S.L. & L.M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68: 619–640.

NSIDC (National Snow and Ice Data Center). 2002. SMEX tower-based radiometric surface temperature, Walnut Creek, Iowa. http://nsidc.org/daac/ Accessed: March 3, 2004.

Persons, M.H. & A.L. Rypstra. 2001. Wolf spiders show graded antipredator behavior in the presence of chemical cues from different sized predators. Journal of Chemical Ecology 27:2493–2504.

Persons, M.H., S.E. Walker, A.L. Rypstra & S.D. Marshall. 2001. Wolf spider predator avoidance tactics and survival in the presence of diet-associated predator cues (Araneae, Lycosidae). Animal Behaviour 61:43–51.

Persons, M.H., S.E. Walker & A.L. Rypstra. 2002. Fitness costs and benefits of antipredator behavior mediated by chemotactile cues in the wolf spider *Pardosa milvina* (Araneae, Lycosidae). Behavioral Ecology 13:386–392.

Sih, A. 1980. Optimal behavior: can foragers balance two conflicting demands? Science 210: 1041–1043.

Stephens, D.W., & J.R. Krebs. 1986. Foraging Theory. Princeton University Press, Princeton, NJ.

Walker, S.E., S.D. Marshall, A.L. Rypstra & D.H. Taylor. 1999a. The effects of hunger on locomotory behaviour in two species of wolf spider (Araneae, Lycosidae). Animal Behaviour 58: 515–520.

Walker, S.E., S.D. Marshall & A.L. Rypstra. 1999b. The effect of feeding history on retreat construction in the wolf spider *Hogna helluo* (Araneae, Lycosidae). Journal of Arachnology 27:689–691.

Manuscript received 30 October 2003, revised 22 March 2004.

2004. The Journal of Arachnology 32:862–865

SHORT COMMUNICATION

DESCRIPTION OF MALE *PHRYNUS ASPERATIPES* (AMBLYPYGI, PHRYNIDAE) FROM BAJA CALIFORNIA SUR, MEXICO

María-Luisa Jiménez and **Jorge Llinas-Gutiérrez**: Laboratorio de Aracnología y Entomología, Centro de Investigaciones Biológicas del Noroeste (CIBNOR) Apdo. Postal 128, La Paz, B.C.S. 23000, México. E-mail: ljimenez04@cibnor.mx

ABSTRACT. The first known male of the whip spider *Phrynus asperatipes* (Wood) is described from two oases and other regions of Baja California Sur, México. It differs from the females as follows: males have the carapace (6.5–7.9 mm) and abdomen (11.0–12.4 mm) smaller than females. Also on an average, the femora (2.3 mm) and tibiae (7.2 mm) of the antenniform legs are shorter than in females.

Keywords: Whip spiders, *Phrynus*, Mexico, Baja California, taxonomy

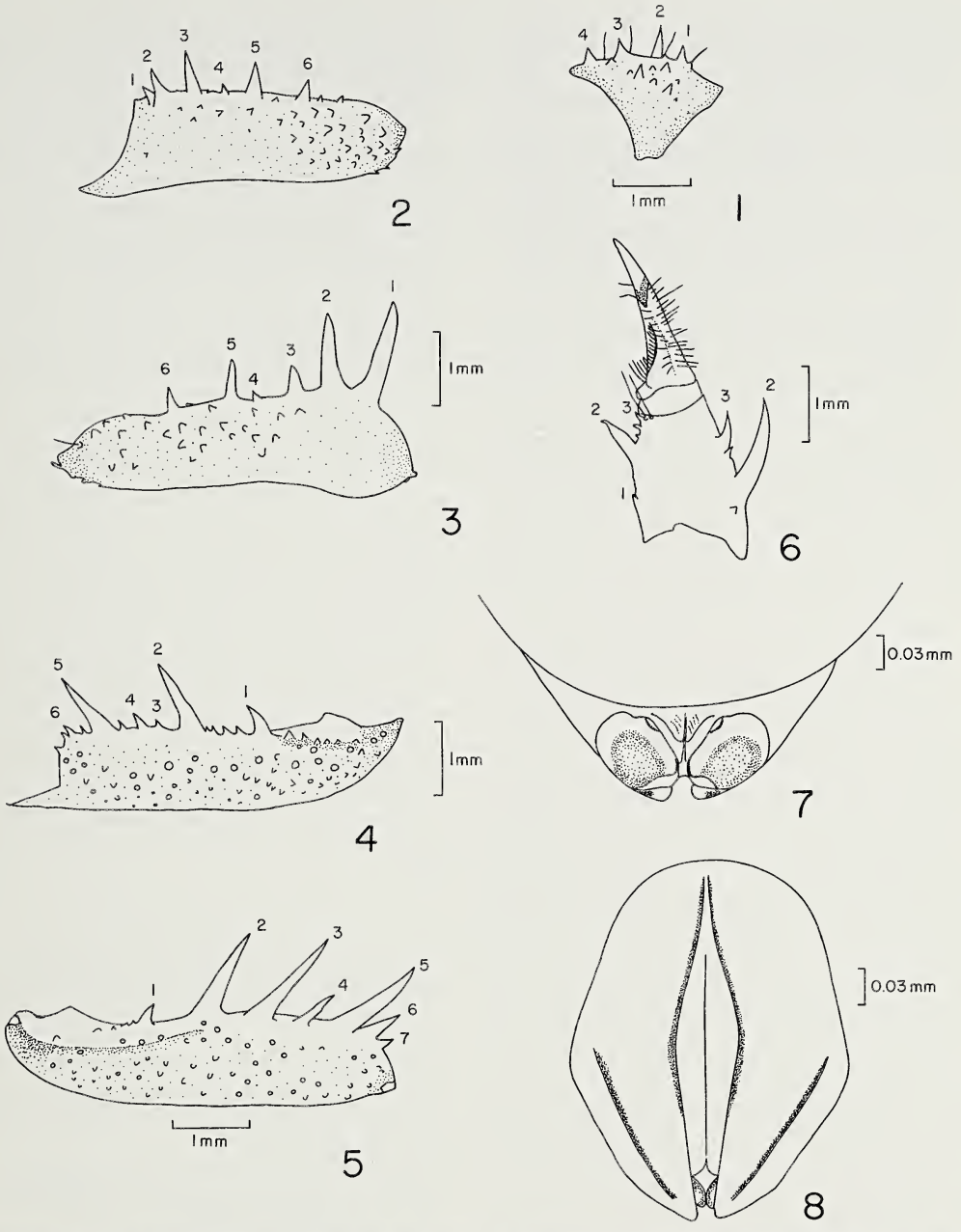
At present, amblypygids of the Baja California Peninsula are represented by two species: *Acanthophrynus coronatus* (Butler 1873) from Sierra de San Lázaro (Quintero 1980) and *Phrynus asperatipes* (Wood 1863) from several localities in the state of Baja California Sur (Quintero 1981; Vázquez-Rojas 1996; Avila-Calvo & Armas 1997). Vázquez-Rojas (1996) agreed with Mello-Leitao (1931), recording *Acanthophrynus spinifrons* (Pocock 1894) from this region. Quintero (1980), in his review of the genus *Acanthophrynus*, considered this species to be synonymous with *A. coronatus*.

Originally, the whip spider *P. asperatipes* was described by Wood (1863) from Baja California, probably from Baja California Sur, México, based on a specimen of sex not determined in the original description and which was lost (Quintero 1981). Kraepelin (1895) determined this species as *Neophrynus whitei* Kraepelin 1895 and later (1899) as *Tarantula whitei*. Quintero (1981), in his review of the genus *Phrynus*, designated a topotypic female as the neotype of *P. asperatipes*. In 1983, he classified *Hemiphrynus machadoi* Fage 1951 from southern Africa in the genus *Phrynus* and considered the former as the sister group to *P. asperatipes*. Weygoldt (1996) in his study on African amblypygids assigned the first species as unique in the genus *Xerophrynus* of the Phrynichidae and tentatively considered it as an ancestral descendant in the line that conduced this family.

Phrynus asperatipes is endemic to Baja California Sur and has been collected from creeks, a palm oasis, under rocks on a hillside and in a sand dune area, representing the most xeric conditions under which a species of *Phrynus* has been found (Quintero 1981). Previously, only females of *P. asperatipes* have been known from Baja California. We here present a description of the first males of this species. The specimens were collected near two oases and from several localities in the central and southern areas of the state of Baja California Sur. The measurements (in mm) were made using a standard ocular grid in a Zeiss dissecting stereomicroscope (Quintero 1981; Armas & Pérez-González 2001). Drawings were made with a camera lucida using magnifications of 1.2–3.2X for the pedipalp, trichobothria and genitalia. Abbreviations were used following Quintero (1981) and Weygoldt (2000). Specimens are lodged in the following institutions: National Collection of Arachnids (CNAN) at the Instituto de Biología, Universidad Autónoma de México; Museum of Comparative Zoology, Harvard University (MCZ), American Museum of Natural History, New York (AMNH); and the Arachnid Collection at the Centro de Investigaciones Biológicas del Noroeste (CARCIB).

Phrynus asperatipes (Wood 1863)
Figs. 1–8

Material examined.—MEXICO: *Baja California Sur*: 4 ♂, La Purísima, 26°12′N, 112°03′W, elevation 291 m, 25 & 27 August 2002, 6 April 2003, I. Posada, G. Nieto, M. Correa (CNAN); 2 ♂, San José Comondú, 26°04′N, 111°49′W, elevation 300 m, 29 September 2002, 7 April 2003, I. Posada, G. Nieto, M. Correa (MCZ); 2 ♂, at 116 and 117 km Transpeninsular Highway 19 (Todos Santos-Cabo San Lucas), 22°55′N, 109°59′W, April–February



Figures 1–8.—*Phrynus asperatipes* Wood, male. 1. Left trochanter, anterodorsal view. 2. Left femur dorsal. 3. Left femur ventral. 4. Left tibia ventral. 5. Left tibia dorsal. 6. Basitarsus and tarsus, inner lateral view. 7. Genitalia ventral view. 8. Genitalia dorsal view.

1988, B. Merrill, D. Ward Jr. (AMNH); 1 ♂, Buena Vista, 23°01′N, 110°11′W, 26 January 1988, V.R. Roth (CARCIB).

Diagnosis.—*Phrynus asperatipes* differs from other species of *Phrynus* in having a distinct suture between the pedipalpal tarsus and post-tarsus, which in ventral view has a "V" form; cleaning organ without a dorso-medial row of minute bristles, basitibia of leg IV not articulated; color of some populations is yellowish brown, not seen in other species of *Phrynus*. As in *P. operculatus* Pocock 1902, *P. asperatipes* has distinct sexual dimorphism in the size of the genital operculum and males have a larger operculum than females.

Description.—*Males (n = 9):* Total length 17.4 mm (13.5–17.8 mm), carapace, chelicerae, and ped-

ipalps yellowish brown. Carapace with two orange-brown spots posterior to the frontal area and five dark spots on each side; frontal area light yellow with a black ocular tubercle rounded with a brown circle; sulcus dark brown from which radiate four shallow grooves. Carapace edge dark orange-brown. Legs 1–4 yellowish brown with many darker setiferous tubercles; patella darker than the other segments. Carapace with uniformly scattered setiferous tubercles. Frontal area narrow, with anterior edge lightly curved and tuberculated; frontal process hidden. Ocular tubercle small 0.7 mm (0.6–0.8 mm), separated 0.5 mm from anterior edge. Lateral eyes separated 3.4 mm (2.8–3.9 mm), by 1.2 mm (0.98–1.47 mm) from the anterior edge and by 1.5 mm (1.5 mm) from the lateral edge of the carapace. Carapace length 6.5 mm (5.5–6.9 mm) and width 10.0 mm (8.3–10.2 mm). Dorsal surface of the basal segment of the chelicerae without distal tubercles; with a single tooth on external margin of basal segment and two ridges. Mobil finger with four teeth in ventral surface. Pedipalps: Trochanter with four anterior spines and setiferous tubercles (Fig. 1). Femur Fd1 small; Fd2 shorter than Fd3, and they do not share a common base; Fd4 smaller than Fd1; Fd5 longer than Fd6; Fv1 longer than Fv2; Fv3 longer than Fv4; Fv5 longer than Fv6 (Figs. 2, 3). Tibia Td1 small; Td2 longer than Td5; Td4 not longer than Td3 and Td6; Tv1 longer than Tv7; Tv2 is not almost the same size as Tv3 but much longer; Tv5 longer than Tv4 and Tv6 (Figs. 4, 5). Basitarsus Bd1 very small, 1/5 part of the size of Bd3; Bv1 and Bv3 small, Bv2 well developed and longer than Bv3 (Fig. 6). Tarsus and post-tarsus of the pedipalp not fused, with a visible suture, that in ventral view, has a "V" form. Femur 5.4 mm (4.4–6.7 mm) long; tibia 6.4 mm (4.5–6.6 mm) long and 1.8 mm (1.8 mm) wide; basitarsus 2.7 mm (2.0–2.7) long and 1.2 mm (1.2–1.8 mm) wide. Tarsus 2.5 mm (2.0–2.5 mm) long. Legs: Second tarsomere of all tarsi without a tranverse line on distal end. Flagellum of the antenniform leg with 92 segments: 29 tibial subarticles and 63 tarsal subarticles. Femur 13.8 mm (10.6–15.6 mm), tibia 23.8 mm (19.3–23.8 mm), tarsus 24.3 mm (20.0–24.3 mm). Leg II: Femur 8.6 mm (8.2–10.0 mm), tibia 8.5 mm (7.6–10.2 mm). Leg III: Femur 9.8 mm (7.6–11.3 mm), tibia 9.5 mm (7.4–11.9 mm). Leg IV: Femur 8.0 mm (6.8–9.8 mm), tibia (5.9/0.1/2.9/4.9) (8.9/1.6/4.0/6.2)-(5.8/0.1/2.5/4.5), tarsus (1.0/0.4/0.1/0.8) (0.8/0.2/0.4/1.1)-(0.6/0.1/0.3/0.7). Basitibia of leg IV not articulated; trichobothrial ratios: bt 0.2, bf 0.1, bc 0.4, sci 1.8. Sternum tripartite, anterior sternite thin and short with three long middle setae and 18 basal setae of different sizes; median and posterior sternites not conspicuous, first with four setae and last with three setae. Abdomen 11.0 mm (7.8–11.0 mm) long, with light yellow segments and two middle darker spots, anterior segment with two brown depressions, lateral sides dark yellow, venter light yellow. Genital operculum 3.8 mm (2.9–3.9 mm) long and 5.4 mm (3.9–5.4 mm) wide with a curved posterior edge; genitalia as in Figs. 7, 8.

Variation.—Coloration from light yellow to dark brown. Measurements of distance of ocular tubercle to external edge of carapace, distance between lateral eyes to lateral edge of carapace and width of pedipalpal tibia were constant. The range of the trichobothria of tibia IV was sbc 0.3–0.4, and sci 0.5–0.6.

Distribution.—This species is known only from Baja California Sur.

Natural history.—Specimens were mainly collected with pitfall traps and by hand under rocks in xeric vegetation surrounding La Purísima and San José Comondú oases and in lesser proportion in mesic vegetation in these localities. Both sexes were more abundant during summer (August–September), although some adults were captured in April. Specimens were more common in San José Comondú than in La Purísima. Some specimens have been seen in houses, where local people call them "vinagrillos" and considered them "poisonous."

We are grateful to Oscar Armendariz for help with the drawings, Carlos Palacios for his help during field collections, and also to the editor and anonymous reviewers for their comments to this manuscript. The editing staff at CIBNOR improved the English text. This paper received financial support from Consejo Nacional de Ciencia y Tecnología (CONACyT) (SEMARTNAT-2002-C01-0052) México.

LITERATURE CITED

Armas, L.F. de & A. Pérez-González. 2001. Los amblipígidos de República Dominicana (Arachnida:Amblypygi). Revista Ibérica de Aracnología 3:47–66.

Avila-Calvo, A.F. & L.F. de Armas. 1997. Lista de los amblipígidos (Arachinida:Amblypygi) de México, Centroamérica y las Antillas. Cocuyo (La Habana) 6:31–32.

Kraepelin, K. 1895. Revision der Tarantuliden Fabr. Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg 13(3):3–53.

Kraepelin, K. 1899. Scorpiones und Pedipalpi. Tierreich 8:I–xiii,1–265.

Mello-Leitão, C. 1931. Pedipalpos do Brasil e algumas notas sobre a Ordem. Arachos Museum Nacional Rio de Janeiro 33:7–72.

Quintero, D. 1980. Systematics and evolution of *Acanthophrynus* Kraepelin (Amblypygi, Phrynidae). Verhandlungen des 8. Internationalen Arachnologen-Kongress, Wien. (J. Gruber ed.). H. Egermann, Wien.

Quintero, D. 1981. The amblypygid genus *Phrynus* in the Americas (Amblypygi, Phrynidae). Journal of Arachnology 9:117–166.

Quintero, D. 1983. Revision of the amblypygid spiders of Cuba and their relationship with the Caribbean and continental American amblypigid fauna. Studies on the Fauna of Curaçao and other Caribbean Islands 65:1–54.

Vázquez-Rojas, I. 1996. Amblypygi. Pp. 71–72. *In* Biodiversidad Taxonomía y Biogeografía de Artrópodos de México: Hacia una síntesis de su conocimiento. (J. Llorente-Bousquets, A. García-Aldrete, E. González-Soriano, eds.). Instituto de Biología, Universidad Nacional Autónoma de México Mexico City, D.F., México.

Weygoldt, P. 1996. The relationships of the south east African whip spiders *Hemiphrynus machadoi* Fage 1951 and *Phrynichus scullyi* Purcell, 1901: introduction of the new generic names *Xerophrynus* and *Phrynichodamon* (Chelicerata: Amblypygi). Zoologischer Anzeiger 235:117–130.

Weygoldt, P. 2000. Whip Spiders. Their Biology, Morphology and Systematics. Apollo Books, Stenstrup.

Wood, H.C. 1863. On the Pedipalpi of North America. Journal of the Academy of Natural Sciences. Philadelphia 5:357–376.

Manuscript received 15 June 2003, revised 23 October 2003.

2004. The Journal of Arachnology 32:866–869

SHORT COMMUNICATION

CONFIRMATION OF PARTHENOGENESIS IN *TITYUS TRIVITTATUS* KRAEPELIN 1898 (SCORPIONES, BUTHIDAE)

Carlos A. Toscano-Gadea: Sección Entomología, Facultad de Ciencias, Iguá 4225 and Laboratorio de Etología, Ecología y Evolución, Instituto de Investigaciones Biológicas Clemente Estable, Avenida Italia 3318. Montevideo, Uruguay. E-mail: cat@fcien.edu.uy

ABSTRACT. The parthenogenesis in *Tityus trivittatus* Kraepelin 1898, is confirmed for the first time, based on the progeny of three virgin females raised in isolation since their birth. The possible and occasional introduction of this species into Uruguay is discussed.

Keywords: Scorpions, asexual reproduction, Uruguay

Just seven species of scorpions, from a total of approximately 1500 known (Fet et al. 2000), have been documented as parthenogenetic. Of these seven species, six belong to the family Buthidae: *Hottentotta hottentotta* (Fabricius 1787), *Ananteris coineaui* Lourenço 1982 (following Lourenço 1994 and Lourenço & Cuellar 1999, respectively) and four species of the neotropical genus *Tityus* Koch 1836: *T. serrulatus* Lutz & Mello 1922, *T. uruguayensis* Borelli 1901, *T. colombianus* (Thorell 1876) and *T. metuendus* Pocock 1897 (Matthiesen 1962; Zolessi 1985; Lourenço 1991 & Lourenço & Cuellar 1999, respectively). However, the unisexual condition of populations of *T. uruguayensis* has been disputed (Toscano-Gadea 2001). The remaining species belongs to Ischnuridae: *Liocheles australasiae* (Fabricius 1775) according to Makioka & Koike (1984, 1985), Makioka (1992, 1993) and Yamazaki et al. (2001). In general, this kind of asexual reproduction can be considered unusual (conversely, see Lourenço 2000).

Tityus trivittatus Kraepelin 1898 is a medium-sized scorpion, growing up to 65 mm long, presenting an orange-yellow or reddish coloration, with three dark brown longitudinal bands that go from tergite I to IV (a detailed description was included in Maury 1970, 1997). The distribution of this species includes Argentina, Paraguay, Brazil and Uruguay; bisexual populations are found in Paraguay, Brazil and northern Argentina (Maury 1970, 1997).

Knowledge of the biology of this species is important due to the possible medical significance of its venom, its synanthropic character and its apparent proclivity for asexual reproduction. The possibility of parthenogenesis in *Tityus trivittatus* was first suggested by Maury (1970, 1997) and later by Peretti (1994, 1997). Maury (1970) suggested that this species is parthenogenetic after finding a disproportionate sex-ratio of 1 male: 145 females. In 1997, the same author surveyed 236 individuals, finding only two males. He also held in isolation two individuals captured in the city of Buenos Aires, Argentina, which gave birth to 8 and 13 young scorpions, respectively, after molting into adulthood. Thus, there is strong indirect evidence of the existence of facultative parthenogenesis in this species. However, as females of *Tityus* can molt after giving birth (Toscano-Gadea 2001), and eventually maintain sperm in their reproductive tract, the progeny obtained by Maury would not necessarily be an evidence of parthenogenesis. Later on, Maury (1997) tried to raise this species in captivity but failed, due to difficulties presented in the breeding. Even raised under strict temperature, humidity and feeding conditions, the scorpions rarely survived for more than the second or third instar.

The objective of this study was to test the parthenogenetic condition of *T. trivittatus* through successive generations and describe the development in captivity of the progeny.

In 1999, one female of *T. trivittatus* was captured in the city of Córdoba, Argentina and donated to the author by Dr. Alfredo Peretti. This female gave birth to sixteen young scorpions in January 2000 and died in February 2001, with eleven scorpions ready to be born. The second instar juveniles were separated from their mother after the first molt, approximately sixteen days after their birth, and from that moment on, were kept in individual Petri dishes

Table 1.—Duration of each juvenile stage in *T. trivitattus* Kraepelin 1898. All the individuals first molted 14–18 days after their birth. The numbers that appear under the second, third and fourth molt columns correspond to intermolt periods. Only the individuals that survived after the second molt were considered. The (—) represents no data available.

Number of the individual	First molt	Second molt	Third molt	Fourth molt
1	14–18 days	299 days	391 days	—
2	14–18 days	297 days	399 days	361 days
3	14–18 days	343 days	349 days	Died; 6 Oct. 2001
4	14–18 days	304 days	Died; 12 Feb. 2001	—
5	14–18 days	342 days	Died; 4 Nov. 2001	—
6	14–18 days	347 days	Died; 12 Feb. 2001	—
7	14–18 days	324 days	Died; 17 April 2001	—
8	14–18 days	295 days	410 days	345 days
9	14–18 days	342 days	368 days	—
Mean	16 days	321.4 days	383.4 days	353 days

of 8.5 cm diameter and 1 cm height. I used flattened soil as substrate (with stones providing refuges) and a fresh water supply. After the second molt, they were placed in bigger containers (9.5 cm diameter x 11 cm height), with the same substrate. In both containers, the substrate was changed every 30–45 days. The alimentation consisted principally of juvenile and adult spiders: *Schizocosa malitiosa* (Tullgren 1905), *Lycosa thorelli* (Keyserling 1877) and *Metaltella simoni* (Keyserling 1877), cockroaches: *Periplaneta americana* (Linnaeus), *Blatta* sp. and *Blattella* sp., and green grasshoppers belonging to the family Decticinidae. All juvenile scorpions were fed at the same time, with the same kind of prey, at least every 15 days. The remnants of prey were immediately taken away to avoid the appearance of fungi and mites. The containers were kept in a room with natural illumination and a temperature of 23.9 °C ± 5.0. The humidity varied from 60–80 %. The female and the individuals that died during their development were deposited in the Arachnological Collection of the Sección Entomología of Facultad de Ciencias, Montevideo.

The results of the juvenile stage duration are shown in Table 1. Seven individuals died before the second molt, four died after the second and one individual died after the third molt. Of the remaining 4, one female (number one) gave birth to twelve offspring after the third molt, produced a second clutch and then died. When she was dissected, only ovaries were found. Two other females (numbers two and eight) gave birth to six and 11 offspring, respectively, after the fourth molt. The remaining individual (number nine), is alive after three molts, without any progeny yet (Table 2). From these data, we are able to confirm the thelytokous parthenogenesis in *T. trivittatus*. This species should be added to the list of parthenogenetic scorpions, increasing the number to eight in this order.

In addition, the second clutch of female number one confirmed the capacity of multiple parturition in *T. trivittatus*, already pointed out by Peretti (1997). According to Polis & Sissom (1990), this peculiarity is shared with the parthenogenetic *T. serrulatus* but probably not with *T. uruguayensis* (Toscano-Gadea 2001 and unpub. data).

Approximately 95% of all living species reproduce sexually (Lourenço 2000). However, parthenogenesis would offer advantages for the species that practice it, namely the foundation of a new population by only one individual and rapid colonization of new habitats (San Martín & Gambardella 1966; Cuellar 1977, 1994; Maury 1997; Lourenço & Cuellar 1995, 1999; Lourenço 2000). *Tityus trivittatus* would appear to be a good colonizer in new environments, based on the possibility of unisexual reproduction, but also because of their ability to reproduce after fewer molts (three or four) than other *Tityus* species as *T. serrulatus* and *T. uruguayensis* which need five molts to become adults (Matthiesen 1962; Zolessi 1985).

The presence of *T. trivitattus* in Uruguay was pointed out by Maury (1997) based on three individuals collected in Colonia, Uruguay ("Estancia del Dr. Rebuffo", 15 km from Colonia City, II-1985, D.J. Carpintero coll.) a neighboring province of Buenos Aires, Argentina, separated only by a narrow section of the Río de la Plata. If we consider the abundant information about scorpions that colonize new areas by anthropogenic means (Goyffon 1992; Lourenço et al. 1994; Lourenço & Cuellar 1995; Toscano-Gadea 1998) and the great quantity of tourists from Argentina that visit the city of Colonia from December–March (similar period of major activity for this species according Maury (1997)) we consider reasonable that this species could have entered Uruguay by human transport. Conversely, there have not been any new records

Table 2.—Development of the progeny of the female *T. trivittatus* Kraepelin 1898, born on the 10th of January 2000. The question mark in the last column for individual number 9 represents no progeny at the present. Only the individuals that survived after the second molt were considered. The (—) represents no data available.

Individual #	First molt	Second molt	Third molt	Fourth molt	Observations
1	14–18 Jan. 2000	12 Nov. 2000	8 Dec. 2001	—	Gave birth to twelve scorpions 1 Jan. 2003 and seven in 3 Mar. 2003
2	14–18 Jan. 2000	10 Nov. 2000	15 Dec. 2001	12 Dec. 2002	Gave birth to six scorpions 9 Mar. 2003
3	14–18 Jan. 2000	26 Dec. 2000	11 Dec. 2001	—	Died; 6 Oct. 2001
4	14–18 Jan. 2000	17 Nov. 2000	—	—	Died; 12 Feb. 2001
5	14–18 Jan. 2000	25 Nov. 2000	—	—	Died; 4 Nov. 2001
6	14–18 Jan. 2000	30 Nov. 2000	—	—	Died; 12 Feb. 2001
7	14–18 Jan. 2000	7 Dec. 2000	—	—	Died; 17 April 2001
8	14–18 Jan. 2000	7 Nov. 2000	23 Dec. 2001	4 Dec. 2002	Gave birth to eleven scorpions 15 Feb. 2003
9	14–18 Jan. 2000	21 Dec. 2000	25 Dec. 2001	—	?

for this species in Uruguay during the last 18 years, and never in the departaments of Maldonado and Rocha, that are the most visited by tourists. Finally, the introduction of this species in Uruguay seems to have been occasional, and the transport method, for the moment, an enigma.

Thanks to Alfredo Peretti for kindly donating the female of *T. trivittatus*, to Fernando Costa for the critical reading of the manuscript and his continuous support, Estrellita Lorier and Alba Bentos for identifying the insects. I am especially grateful to Anita Aisenberg for her help with the English and two anonymous reviewers for their helpful comments.

LITERATURE CITED

Cuellar, O. 1977. Animal parthenogenesis. Science 197:837–843.

Cuellar, O. 1994. Biogeography of parthenogenetic animals. Biogeographica 70:1–13.

Fet, V., W.D. Sissom, G. Lowe & M.E. Braunwalder. 2000. Catalog of the scorpions of the world (1758–1998). The New York Entomological Society, New York, 690 pp.

Goyffon, M. 1992. Le role de l'homme dans léxpansion territoriale de quelques espèces de scorpions. Bulletin de la Societé Zoologique, France 117:15–19.

Lourenço, W.R. 1991. Parthenogenesis in the scorpion *Tityus colombianus* (Thorell) (Scorpiones: Buthidae). Bulletin of the British Arachnological Society 8:274–276.

Lourenço, W.R. 2000. Reproduction in scorpions, with special reference to parthenogenesis, Pp. 71–85. *In* Proceedings of the 19th. European Colloquium of Arachnology. (S. Toft & N. Scharff, eds.).

Lourenço, W.R. & O. Cuellar. 1995. Scorpions, scorpionism, life history strategies and parthenogenesis. Journal of Venomous Animal and Toxins 1:51–62.

Lourenço, W.R. & O. Cuellar. 1999. A new all-female scorpion and the first probable case of arrhenotoky in scorpions. Journal of Arachnology 27:149–153.

Lourenço, W.R., M. Knox & M. Yoshizawa. 1994. L'invasion d'une communautè au stade initial d'une succession secondaire par une espèce parthènogenetique de scorpion. Biogeographica 70: 77–91.

Makioka, T. 1992. Reproductive biology of the viviparous scorpion, *Liocheles australasiae* (Fabricius) (Arachnida, Scorpiones, Ischnuridae) II. Repeated pregnancies in virgins. Invertebrate Reproduction and Development 21:161–166.

Makioka T. 1993. Reproductive biology of the viviparous scorpion, *Liocheles australasiae* (Fabricius) (Arachnida, Scorpiones, Ischnuridae) IV. Pregnancy in females isolated from infancy, with

notes on juvenile stage duration. Invertebrate Reproduction and Development, 24:207–212.

Makioka, T. & K. Koike. 1984. Parthenogenesis in the viviparous scorpion, *Liocheles australasiae*. Proceedings of the Japanese Academy, ser B, 60: 374–376.

Makioka, T. & K. Koike. 1985. Reproductive biology of the viviparous scorpion, *Liocheles australasiae* (Fabricius) (Arachnida, Scorpiones, Scorpionidae). I. Absence of males in two natural populations. International Journal of Invertebrate Reproduction and Development 8:317–323.

Matthiesen, F.A. 1962. Parthenogenesis in scorpions. Evolution 16:255–256.

Maury, E.A. 1970. Redescripción y distribución en la Argentina de *Tityus trivittatus trivittatus* Kraepelin 1898 (Scorpiones, Buthidae). Comentarios sobre sus hábitos domiciliarios y su peligrosidad. Physis 29:405–421.

Maury, E.A. 1997. *Tityus trivittatus* en la Argentina. Nuevos datos sobre distribución, partenogénesis, sinantropía y peligrosidad (Scorpiones, Buthidae). Revista del Museo Argentino de Ciencias Naturales 24:1–24.

Peretti, A.V. 1994. Comportamiento de relación madre-cría de *Tityus trivittatus* Kraepelin, 1898 (Scorpiones, Buthidae). Boletín de la Sociedad de Biología de Concepción 65:9–21.

Peretti, A.V. 1997. Alternativas de gestación y producción de crías en seis escorpiones argentinos (Scorpiones: Buthidae, Bothriuridae). Iheringia 82:25–32.

Polis G.A. & W.D. Sissom. 1990. Life history. Pp. 161–223. *In* The Biology of Scorpions (G.A. Polis ed.) Stanford University Press, Stanford.

San Martin P. & L.A. de Gambardella. 1966. Nueva comprobación de la partenogénesis en *Tityus serrulatus* Lutz e Mello-Campos 1922. Revista de la Sociedad Entomológica Argentina XXVIII: 79–84.

Toscano-Gadea, C.A. 1998. *Euscorpius flavicaudis* (Degeer, 1778) in Uruguay: first record from the New World (Scorpiones, Chactidae). Newsletter of the British Arachnological Society 81:6.

Toscano-Gadea, C.A. 2001. Is *Tityus uruguayensis* Borelli, 1901 really parthenogenetic? Pp. 359–364. *In* Scorpions 2001: In Memoriam of Gary A. Polis. (V. Fet & P. Selden, eds.). British Arachnological Society, Burnham Beeches, Bucks.

Yamazaki K., H. Yahata, N. Kobayashi & Makioka T. 2001. Egg maturation and parthenogenetic recovery of diploidy in the scorpion *Liocheles australasiae* (Fabricius) (Scorpions, Ischnuridae). Journal of Morphology 247:39–50.

Zolessi, L.C. de. 1985. La partenogénesis en el escorpión amarillo *Tityus uruguayensis* Borelli 1901 (Scorpionida: Buthidae). Revista de la Facultad de Humanidades y Ciencias, Montevideo, 3ª. Época, Ciencias Biológicas 1:25–32.

Manuscript received 31 March 2003, revised 17 October 2003.

2005. The Journal of Arachnology 33:870–872

SHORT COMMUNICATION

ALLOMETRY OF GENITALIA AND FIGHTING STRUCTURES IN *LINYPHIA TRIANGULARIS* (ARANEAE, LINYPHIIDAE)

Sebastian Funke: Pastor-Fischer Weg 6, 58708 Menden, Germany.

Bernhard A. Huber[1]: Zoological Research Institute and Museum Alexander Koenig, Adenauerallee 160, 53113 Bonn, Germany. E-mail: b.huber.zfmk@uni-bonn.de

ABSTRACT. Allometric scaling is a powerful approach for studying the relationship between size, shape and function. We studied allometric slopes in *Linyphia triangularis*, measuring two male and one female genital characters and several male and female non-genital characters including male chelicerae that are used for fighting. As predicted from theory, genitalia had the lowest allometric values, fighting structures the highest.

Keywords: Copulatory organs, sexual selection, *Linyphia*, allometry

"Mr. Locket tells me that, from preliminary investigations . . . of males of the species *Linyphia triangularis* . . . he does not believe that large specimens have relatively larger jaws than smaller specimens" (Bristowe 1929: 339).

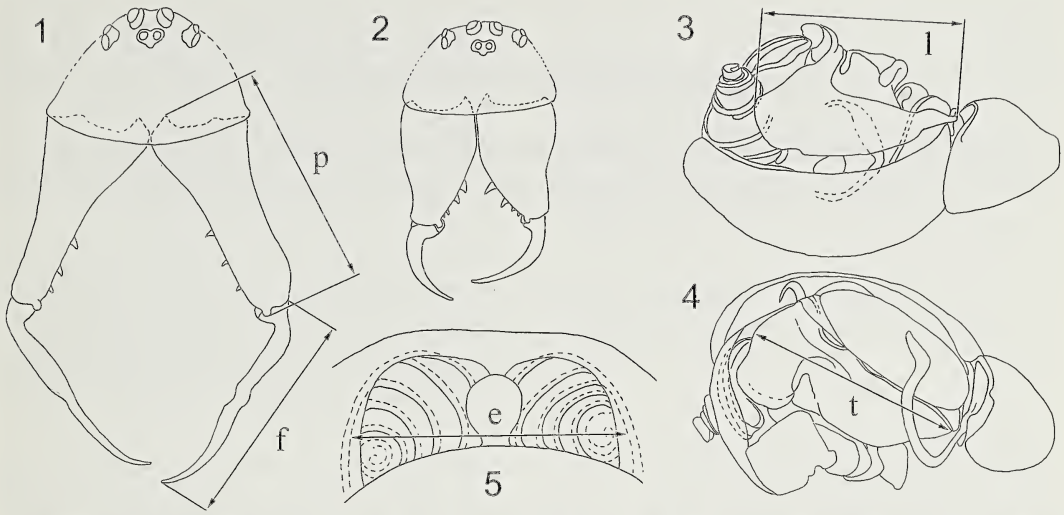
In most animals studied, structures used as weapons or display devices show steeper regression slopes (higher allometric values) than other body parts in relation to body size (Tatsuta et al. 2001; Eberhard 2002a; further references in Eberhard 2002b). This may result from small individuals having relatively little to gain from investing in such structures (Baker & Wilkinson 2001). In contrast, genitalia often have remarkably low slopes (Eberhard et al. 1998; Palestrini et al. 2000; Tatsuta et al. 2001; Kato & Miyashita 2003), presumably resulting from selection to fit all variants of the opposite six ('one-size-fits-all' model, Eberhard et al. 1998). This short note focuses on the relationships between chelicerae (fighting structures), genitalia and body size in *Linyphia triangularis* (Clerck 1757).

Adult males and females of the holarctic *L. triangularis* appear from July to late August with males molting to maturity about 1–3 weeks earlier than females (Toft 1989; Stumpf & Linsenmair 1996). First male sperm precedence has been documented in closely related species (Watson 1991; Stumpf & Linsenmair 1996) and this probably explains mate-guarding of penultimate females (Toft 1989; Stumpf & Linsenmair 1996). Despite the existence of an alternative male mating strategy, where the smaller male attempts to induce the dominant male to leave the female by chasing him out of the web ('interference strategy', Nielsen & Toft 1990), observations on this and a related species (Rovner 1968; Stumpf & Linsenmair 1996; Watson 1990) suggest that fighting ability largely predicts reproductive success. *Linyphia triangularis* males use their chelicerae in aggressive interactions (Rovner 1968) leading to the prediction that these should be under strong directional selection.

Our measurements are based on a sample of 33 adult cohabiting male/female pairs collected in Austria (Upper-Austria, Walding, 48°21′N, 14°12′E, 4 August 2003). The spiders are deposited at the Zoological Research Institute and Museum Alexander Koenig (ZFMK), Bonn. We measured male and female carapace length and width, abdomen length and width, tibia 1 length, paturon and cheliceral fang lengths, as well as epigynum width and the length of two bulbal structures, lamella and tegulum (Figs. 1–5). Measurements were to the nearest 0.01 mm (genitalia)–0.03 mm (legs). Statistical analysis was made with SPSS 11.0, using both ordinary least squares (OLS) and reduced major axis (RMA) regressions of log-transformed data. Carapace width was taken as an indicator of body size, i.e. all OLS regression values are of the respective structure on log carapace width. Both regression techniques supported the same conclusions, so we will present OLS values only.

Our data clearly show the dichotomy between fighting structures and genitalia. The slopes of male chelicerae (paturon: 1.740, fang: 2.319, both $P < 0.001$) were high in comparison to the slopes of tibia and opisthosoma measures (0.607–0.973, $P < 0.003$). Interestingly, female chelicerae also had rel-

[1] Corresponding author.



Figures 1–5.—*Linyphia triangularis*, illustrations of some of the characters measured. 1, 2. Frontal views of large male and medium size female, drawn at same scale. 3, 4. Left genital bulb, prolateral (3) and retrolateral (4) views. 5. Epigynum, posterior view. e = epigynum width, f = fang length, l = bulbal lamina length, p = paturon length, t = tegulum length.

atively steep slopes, though much lower than in males (paturon: 1.070, fang: 1.410, both $P < 0.001$). Genitalia, on the other hand, showed very low slopes for both bulbal structures (lamella: 0.296, $P < 0.001$, tegulum: 0.257, $P = 0.004$), and for the epigynum (0.422, $P = 0.016$). Evidently, there is stabilizing selection on standard size genitalia in *L. triangularis* like in many other arthropods (Eberhard et al. 1998).

Apart from these main results, we incidentally found a surprising relationship between male and female sizes: males (carapace width) in our sample were not larger than females (paired t-test, $P = 0.30$). Lång (2001), working on Swedish populations of the same species, reported that males were on average 5–22% larger than females in 11 out of his 12 samples. We suggest that the absence of body size dimorphism in our sample might be explained by a bias in our sample. We collected only cohabiting adult pairs, i.e. females that were probably non-virgin. If *L. triangularis* has first male sperm precedence like its close relatives (Watson 1991; Stumpf & Linsenmair 1996), then the females in these pairs had a lower reproductive value than virgin females. Large, dominant males might rather invest in searching for virgin females, so we might have missed them. Apart from explaining the absence of a sexual size dimorphism in carapace width in our sample, this finding hints to yet another alternative mating strategy of smaller males: small males might employ a post-copulation cohabitation strategy to profit from the residual female reproductive value that is left for second males in *Linyphia*.

LITERATURE CITED

Baker, R.H. & G.S. Wilkinson. 2001. Phylogenetic analysis of sexual size dimorphism and eye-span allometry in stalk-eyed flies (Diopsidae). Evolution 55:1373–1385.

Bristowe, W.S. 1929. The mating habits of spiders, with special reference to the problems surrounding sex dimorphism. Proceedings of the Zoological Society 21:309–357.

Eberhard, W.G. 2002a. The relation between aggressive and sexual behavior and allometry in *Palaeosepsis dentatiformis* (Diptera: Sepsidae). Journal of the Kansas Entomological Society 75: 317–332.

Eberhard, W.G. 2002b. Natural history and behavior of *Chymomyza mycopelates* and *C. exophthalma* (Diptera: Drosophilidae), and allometry of structures used as signals, weapons, and spore collectors. Canadian Entomologist 134: 667–687.

Eberhard W. G., B.A. Huber, R.L. Rodriguez S., R.D. Briceño, I. Salas and V. Rodriguez. 1998. One size fits all? Relationships between the size and degree of variation in genitalia and other body parts in twenty species of insects and spiders. Evolution 52:415–431.

Kato, N. & T. Miyashita. 2003. Sexual difference in modes of selection on the pleopods of crayfish (Decapoda: Astacoidea) revealed by the allometry of developmentally homologous traits. Canadian Journal of Zoology 81:971–978.

Lång, G.H.P. 2001. Sexual size dimorphism and juvenile growth rate in *Linyphia triangularis* (Lin-

yphiidae, Araneae). Journal of Arachnology 29: 64–71.

Nielsen, N. & S. Toft. 1990. Alternative male strategies in *Linyphia triangularis* (Araneae, Linyphiidae). Acta Zoologica Fennica 190:293–297.

Palestrini, C., A. Rolando & P. Laiolo. 2000. Allometric relationships and character evolution in *Onthophagus taurus* (Coleoptera: Scarabaeidae). Canadian Journal of Zoology 78:1199–1206.

Rovner, J.S. 1968. Territoriality in the sheet-web spider *Linyphia triangularis* (Clerck) (Araneae, Linyphiidae). Zeitschrift für Tierpsychologie 25: 232–242.

Stumpf, H. & K.E. Linsenmair. 1996. Observations on the mating systems of two spiders, *Linyphia hortensis* Sund. and *L. triangularis* (Cl.) (Linyphiidae: Araneae). Revue Suisse de Zoologie, vol. hors série (August 1996):627–634.

Tatsuta, H., K. Mizota & S.-I. Akimoto. 2001. Allometric patterns of heads and genitalia in the stag beetle *Lucanus maculifemoratus* (Coleoptera: Lucanidae). Annals of the Entomological Society of America 94:462–466.

Toft, S. 1989. Mate guarding in two *Linyphia* species (Araneae: Linyphiidae). Bulletin of the British arachnological Society 8:33–37.

Watson, P.J. 1990. Female-enhanced male competition determines the first mate and principal sire in the spider *Linyphia litigiosa* (Linyphiidae). Behavioral Ecology and Sociobiology 26:77–90.

Watson, P.J. 1991. Multiple paternity and first mate sperm precedence in the sierra dome spider, *Linyphia litigiosa* Keyserling (Linyphiidae). Animal Behaviour 41:135–148.

Manuscript received 10 March 2004, revised 10 June 2004.

2005. The Journal of Arachnology 33:873–877

SHORT COMMUNICATION

MATRIPHAGY IN THE NEOTROPICAL PSEUDOSCORPION *PARATEMNOIDES NIDIFICATOR* (BALZAN 1888) (ATEMNIDAE)

Everton Tizo-Pedroso and **Kleber Del-Claro**: Laboratório de Ecologia Comportamental e de Interações, Instituto de Biologia, Universidade Federal de Uberlândia. C.P.593, Cep 38400-902, Uberlândia, MG, Brasil. Telfax: 55(34)32182243. E-mail: delclaro@ufu.br.

ABSTRACT. We studied the natural history and social behavior of *Paratemnoides nidificator* (Balzan 1888) in a tropical savanna system. Females were responsible for all nymphal care. We observed, for the first time in pseudoscorpions, the occurrence of matriphagy behavior by the offspring. During conditions of food deprivation, the mother went out of the nest and passively awaited the protonymphs' attack, not reacting to the capture nor to the nymphs feeding on her body. We suggest that this extreme form of parental care, matriphagy, can reduce cannibalism among protonymphs and facilitate the evolution of social behavior in pseudoscorpions.

RESUMO. Nós estudamos a história natural e o comportamento social de *Paratemnoides nidificator* (Balzan 1888) na região dos cerrados. As fêmeas foram responsáveis por todo o cuidado às ninfas. Nós observamos, pela primeira vez em pseudoescorpiões, a ocorrência de matrifagia pela prole. Em condições de fome, a mãe deixa o ninho e passivamente espera que as protoninfas a ataquem, não reagindo nem à captura, nem à alimentação das ninfas sobre seu corpo. Nós sugerimos que esta forma extrema de cuidado parental, matrifagia, possa reduzir o canibalismo entre as protoninfas e assim facilitar a evolução de comportamento social em pseudoescorpiões.

Keywords: Social behavior, maternal care, Arachnida, cannibalism, tropical savanna

The order Pseudoscorpiones is highly diversified with more than 3,239 described species in 425 genera and 24 families, representing around 3.3% of all arachnids (Harvey 1991, 2002). In general, pseudoscorpions are small (2–8 mm) and are non-social animals that behave aggressively in intraspecific contacts (Weygoldt 1969; Zeh 1987). Zeh (1987) reported fights between males of a Chernetidae species during contests for food or females, resulting in cannibalism. Some Atemnidae species, however, show a high level of sociality, living in groups, sharing food and hunting cooperatively (Brach 1978; Zeh & Zeh 1990).

All pseudoscorpion species present some level of parental care. Indeed, females of all species take care of embryos that are maintained inside a brood sac attached to her genital opening (Levi 1953; Gabutt 1970b; Weygoldt 1969). Females can also build silk chambers in which they rest with the brood sac until the emergence of the protonymphs (Brach 1978; Gabbutt 1962, 1966, 1970a; Levi 1948, 1953; Harvey 1986; Zeh & Zeh 2001). In *Neobisium maritimum* (Leach 1812) the silk chamber is built and occupied by one individual, and several chambers may occur in the same rock fissure (Gabbutt 1962, 1966). Females of *Neobisium muscorum* (Leach 1817) can have chambers placed side by side (Weygoldt 1969). In *Paratemnoides elongatus* (Banks 1895) and *P. minor* (Balzan 1892), both species that occur beneath tree bark, nymphs can build molt chambers cooperatively and adult females bearing a brood sac can use molt chambers for brood care as well (Brach 1978; Hahn & Matthiesen 1993b). This cooperative building of nests saves time and silk, maintains appropriate humidity conditions and protects the brood from predators (Brach 1978). In both those *Paratemnoides* species females in the nest remove the brood sac from the genital opening after secreting the nutritive fluid to the embryos (Brach 1978; Hahn & Matthiesen 1993a). Protonymphs of *Pselaphochernes scorpioides* (Herman 1804) remain 2–3 days inside the nest receiving care until they disperse (Weygoldt 1969).

Pseudoscorpions are widespread. For instance, in Central Amazon, Adis & Mahnert (1985) recorded 60 species belonging to 25 genera in 10 families. The Brazilian cerrado savanna originally covered approximately 25% of the country and is currently

Table 1.—Composition of all colonies (by sex and age classes) of *Paratemnoides nidificator* (Atemnidae) studied.

Colony	Males	Females	Tritonymphs	Deutonymphs	Protonymphs	Total
1	3	4	8	—	—	15
2	4	5	16	14	3	42
3	8	12	15	5	—	40
4	7	5	4	12	21	49
5	9	10	4	—	—	23
6	4	7	1	28	30	70
7	12	11	7	3	—	33
X ± SD	6.71 ± 3.25	7.71 ± 3.25	7.85 ± 5.7	8.86 ± 10.08	7.71 ± 12.47	38.86 ± 17.98

one of the most endangered tropical ecosystems (Oliveira & Marquis 2002). To our knowledge there is no study about pseudoscopions in the cerrado. Here, we studied the biology and natural history of *Paratemnoides nidificator* (Balzan 1888) an atemnid species that occurs under the bark of living trees of *Caesalpinia pelthophoroides* (Caesalpiniaceae), a tree found throughout the cerrado domain.

Observations for this study were conducted from October 2001 to December 2003 in Uberlândia, Brazil (18° 53′S, 48° 15′W; 863 m el.), in the southeastern limit of the cerrado distribution. Seven colonies of pseudoscorpions (Table 1) were collected from the field and maintained in captivity during all the study. Each colony was kept in a glass bottom culture dish (12 cm of diameter) having the original piece of tree bark and was fed twice a week with live termites (*Armithermes* sp.) and beetles (*Acanthocelides obtectus*, Bruchidae). Moisture was provided by a small piece of water-soaked cotton. Behavioral observations were made using the "all occurrence samples" method (Altmann 1974). Using this method, everything that a group or individual does during an observation session is recorded *ad libitum*. This method is particularly useful to begin a study or to observe rare or fortuitous behaviors (see also Martin & Bateson 1993; Del-Claro 2004). Individual observation sessions lasted 30–40 min and were made during the day (mainly between 09:00h and 15:00h) using natural light. As colonies are built under the bark of trees, during the observation sessions the petri dishes with the colonies were put on a wire stand with a mirror below that enable the observations without be disturbing the animals. In the present paper we describe the social and reproductive behavior of *P. nidificator* based on 50 observation sessions (34 hours total observations). Voucher specimens have been lodged with the Museu de Zoologia de São Paulo (MZUSP).

We observed that females wove the reproductive nest alone. Inside the chambers, the female provided parental care continuously to embryos and nymphs by feeding and grooming them. This lasted until the nymphs were adults or were forced from the nest. The female also guarded the nest entrance against enemies. In some cases, the female produced an additional brood and then forced nymphs from the first brood out of the chamber by touching them with her pedipalps. After chasing the original brood, the female sealed the exit with new silk and produced the new brood sac. The "displaced" nymphs then cooperatively built another chamber in which they molted. The reproductive and the molting chambers were built side by side sharing the vertical walls. This behavior has also been observed in *P. elongatus* (Banks 1895) and *P. minor* (Balzan 1892) (Brach 1978; Hahn & Matthiesen 1993a). In the field, we found colonies of *P. nidificator* with nests composed of 3–20 chambers.

We identified 95 distinct behavioral acts, of which 16 were related to reproductive behavior, mainly parental care (Table 2). Parental behaviors comprised 10.13% of the behaviors seen in this species. However, the acts in this category are performed only by adult females, so more than 75% of adult female behaviors are related to taking care of embryos and young. Other important behavioral acts of females were self-grooming and feeding. Males directly cooperated in parental care by catching and offering prey to all members of the colony (94 records during 50 observation sessions). However, nymphs in general were fed by the mother. Our data revealed that females left the nest to hunt prior to feeding the brood (56%, or in 42 out of 75 times that we observed females leaving the nest during the observations). The mother ate the rest of the carrion left by the nymphs. Tritonymphs hunted cooperatively with the mother (3 in 42 observations of the mother hunting), or without the mother (n = 14 records during 50 observation sessions).

At the end of our observations we recorded colony behavior under food deprivation by depriving the colony food for one week. On the seventh day we observed matriphagy behavior in three of the seven colonies. The mother exited the nest, raised her pedipalps and passively waited for her nymphs to attack. Nymphs (9 ± 3 protonymphs, X ± SD,

Table 2.—Behavioral acts of *Paratemnoides nidificator* (Atemnidae) associated with "Parental Care". Data recorded from a clutch of 90 individuals (33 adults and 57 nymphs) reared in captivity (n = 34 hours of observations).

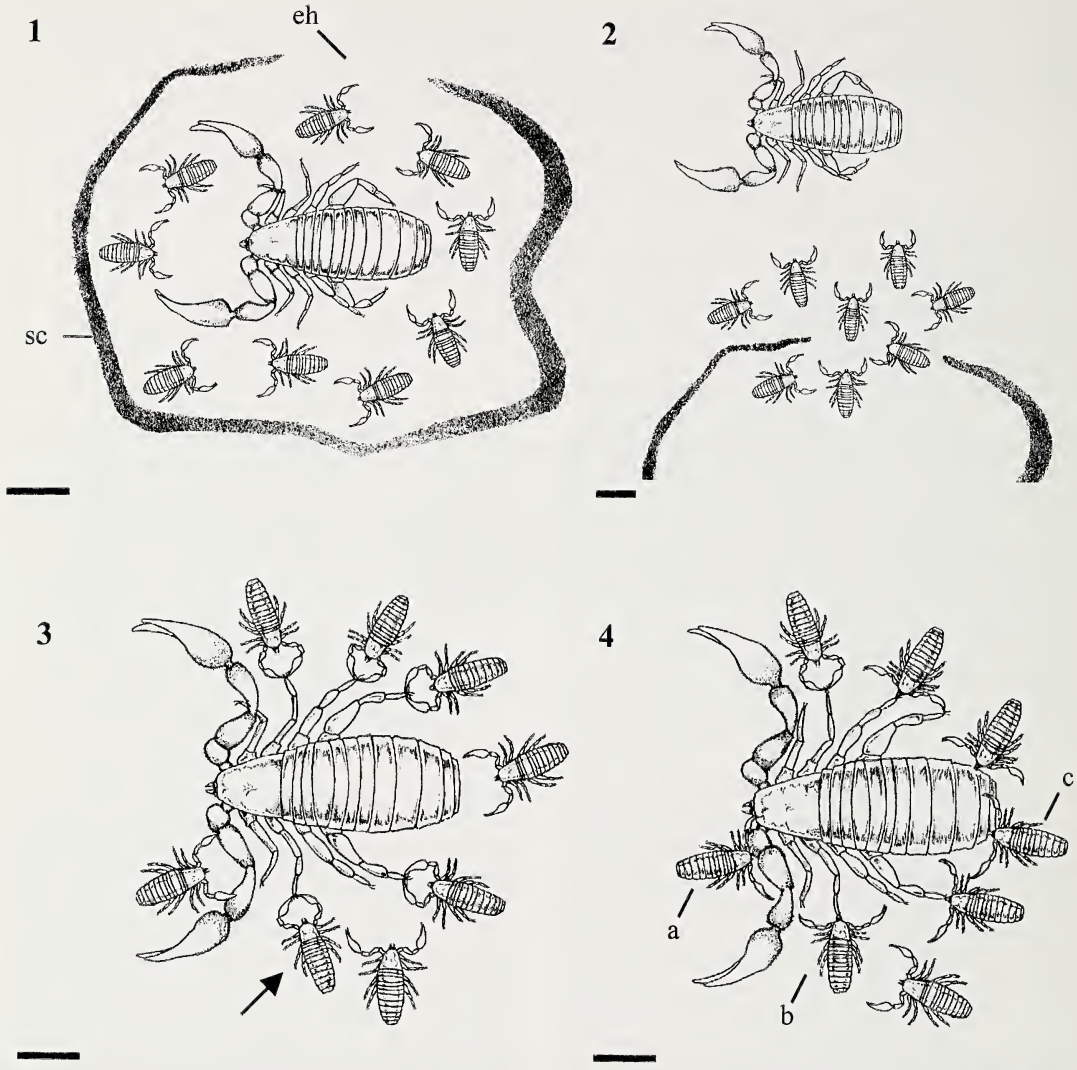
Behavioral act	Number of observations	Percent frequency of the behavioral act (total 453 acts)
1-Female weaving chamber.	179	30.4
2-Female occupying a woven chamber previously built by another individual.	5	0.85
3-Female excluding conspecifics from chamber.	4	0.68
4-Female resting in the nest.	76	12.9
5-Female moving in the nest.	19	3.23
6-Female touching the nest wall with pedipalps.	10	1.7
7-Female touching the embryos with pedipalps.	84	14.3
8-Female touching the protonymphs with pedipalps.	29	4.92
9-Female transporting wood pieces inside the nest.	4	0.68
10-Female inserting fragments of wood in the nest walls.	4	0.68
11-Female stopping in the nest above in second instar embryos.	4	0.68
12-Female stopping in the nest together with the protonymphs.	29	4.92
13-Female excluding conspecifics from previously built chamber.	3	0.51
14-Matriphagy.	3	0.51
15-Female bringing food to her nymphs	42	7.13
16-Males offering prey to nymphs	94	16
Total	589	100

n = 3) left the nest and gathered around the mother and attacked by grasping the mother's legs and pedipalps (3 ± 1 min, X ± SD, n = 3; time to attack). The young fed through the leg joints of the mother. The mother remained motionless as she was consumed (40 ± 5 min, X ± SD, n = 3; time used by nymphs feeding on mother's body, Figs. 1–4). Immediately, in the next step, the mother's exoskeleton was thrown out of the bark piece by the nymphs. Without the mother, nymphs began to hunt cooperatively.

In the classic definition of degrees of social behavior by Wilson (1971), eusocial species are characterized as having members of the same generation using a composite nest, cooperation in brood care, overlap of generations with offspring assisting parents and reproductive division of labor. In *P. nidificator* we did not identify a worker caste. Nevertheless, we consider this pseudoscopion as a permanent social species. In arachnids, Plateaux-Quénu et al. (1997) defined as permanent social species, "a group of individuals of both sexes generally with overlapping generations which cooperate in the construction of a common nest, prey capture and care of the young." These authors consider permanent social species as synonymous with cooperative, non-territorial permanently social species (Plateaux-Quénu et al. 1997).

The trade off between individual sacrifice and colony welfare is well evident in the case of defense, and sometimes this altruistic behavior is accompanied by anatomical specialization (Hölldobler & Wilson 1990). The presence of a sting, used to defend the colony against vertebrates in the honey bees, some genera of ants, social polistine and polybiine wasps, constitutes a remarkable example of convergence in social behavior (Hermann & Blum 1981). There is no anatomical specialization in *P. nidificator* or other arachnids to facilitate matriphagy. However, the simple occurrence of matriphagy in pseudoscorpions and other invertebrates (e.g. Evans et al. 1995; Kim et al. 2000), can be also pointed out as example of convergence in social behavior.

According to Evans et al. (1995), extreme forms of parental care, such as matriphagy, may be frequent among spiders that typically produce single clutches. We did additional laboratory observations in 38 colonies of *P. nidificator* during the reproductive season of 2003. Of these 38 colonies, in 7 the female was maintained alone and she was able to produce only one brood. In the other 31 colonies, females were maintained in the colony and they produced two or more additional clusters, in general three (n = 26). The observation that females alone did not produce additional broods suggests that solitary females may have a smaller reproductive output than that females living in groups. We suggest that the social life in *P. nidificator*, with adults hunting cooperatively, can reduce the chances of cannibalism and improve reproductive conditions for many individuals. In Araneae, Elgar & Crespi



Figures 1–4.—Schematic illustrations of matriphagy in the pseudoscorpion *Paratemnoides nidificator*. 1. Female and protonymphs resting inside the silk chamber (sc), near entrance hole (eh); 2. The mother goes out to the nest and raises her pedipalps. The brood begin to leave the nest; 3. Nymphs gather around the mother and attack by grasping the mother's legs (arrow) and pedipalps; 4. The young feed through the joints of mother's pedipalps (a), legs (b) and abdome (c). Scale = 1.0 mm.

(1992) suggested that by reducing cannibalism among groups of siblings, matriphagy may facilitate the evolution of social behavior (Crespi 1992). We suggest that here also, matriphagy may be an important part of the evolution of sociality in this group.

To our knowledge this is the first record of matriphagy in pseudoscorpions and *P. nidificator* serves as a good model for the difficult assessment of the costs and benefits of altruistic behavior (Krebs & Davies 1993). Further studies could help to clarify proximate and evolutionary causes of matriphagy in pseudoscorpions. Many questions deserve further research. For example, do nymphs survive better as a consequence of matriphagy? Does matriphagy occur in starving colonies in the same mannner as it occurs with isolated females? Could the *P. nidificator* mother be maximiting her ultimate number of offspring by this extreme form of altruism, similar to that reported to spiders (Kim et. al 2000)? These and other questions confirm there is still much to be learned.

We thank Gail Stratton, Heraldo L. Vasconcelos, Paula E. Cushing, Paulo E. Oliveira, Paulo S. Oliveira, Peter Weygoldt, Renata de Andrade as well as an anonymous reviewer, for helpful comments

on the manuscript. We thank Paula E. Cushing also for suggesting further questions to this study. We thank Volker Manhert for identifing the pseudoscorpion, Luciana Zukovski for identifing the beetle and Jorge J. de Faria Neto for drawings. We thank CNPq and Fapemig for financial support.

LITERATURE CITED

Adis, J. & V. Mahnert. 1985. On the natural history and ecology of pseudoscorpioes (Arachnida) from an Amazônian blackwater inundation forest. Amazoniana 9(3):297–314.

Altmann, J. 1974. Observational study of behaviour: sampling methods. Behaviour 49:227–265.

Brach, V. 1978. Social behavior in the pseudoscorpion *Paratemnus elongatus* (Banks) (Pseudoscorpionida: Atemnidae). Insectes Sociaux 25(1): 3–11.

Crespi, B.J. 1992. Cannibalism and trophic eggs in subsocial and eusocial insects. Pp 176–213. *In* Cannibalism: Ecology and Evolution Among Diverse Taxa. (Elgar, M.A. & B.J. Crespi, eds.). Oxford University Press.

Del-Claro, K. 2004. Comportamento Animal: Uma Introdução à Ecologia Comportamental. Editora e Livraria Conceito, Jundiaí. 132pp.

Elgar, M.A. & B.J. Crespi. 1992. Ecology and evolution of cannibalism. Pp 1–12. *In* Cannibalism: Ecology and Evolution Among Diverse Taxa. (Elgar, M.A. & B.J. Crespi, eds.). Oxford University Press.

Evans, T.A., E.J. Wallis & M.A. Elgar. 1995. Making a meal of mother. Nature 376:299.

Gabbutt, P.D. 1962. 'Nests' of the marine false-scorpion. Nature 196:87–89.

Gabbutt, P.D. 1966. An investigation of the silken chambers of the marine pseudoscorpion *Neobisium maritimum*. Journal of Zoology 149:337–343.

Gabbutt, P.D. 1970a. Sampling problems and the validity of life history analyses of pseudoscorpions. Journal of Natural History 4:1–15.

Gabbutt, P.D. 1970b. The external morphology of the pseudoscorpion *Dactylochelifer latreillei*. Journal of Zoology 160:313–335.

Hahn, N.S. & F.A. Matthiesen. 1993a. Desenvolvimento pós-embrionário de *Paratemnus minor* (Pseudoscorpiones, Atemnidae). Revista Brasileira de Biologia 53(3):345–353.

Hahn, N.S. & F.A. Matthiesen. 1993b. Notas biológicas sobre *Paratemnus minor* (Pseudoscorpiones, Atemnidae). Revista Brasileira de Biologia 53(4):571–574.

Harvey, M.S. 1986. The systematics and biology of pseudoscorpions. Pp. 75–85. *In* Australian Arachnology. (Austin, A.D. & N.W. Heather). Australian Entomological Society, Brisbane.

Harvey, M.S. 1991. Catalogue of the Pseudoscorpionida. Manchester University Press, Manchester.

Harvey, M.S. 2002. The neglected cousins: What do we know about the smaller arachnid orders? Journal of Arachnology 30:357–372.

Hermann, H.R. & M.S. Blum. 1981. Defensive mechanisms in the social Hymenoptera. Pp 77–197. *In* Social Insects. Vol. 2. (Hermann H.R., ed.). Academic Press, New York.

Hölldobler, B. & E.O. Wilson. 1990. The Ants. The Belknap Press of Harvard University Press, Cambrigde. 732pp.

Kim, K.W., C. Roland & A. Horel. 2000. Functional value of matriphagy in the spider *Amaurobius ferox*. Ethology 106:729–742.

Krebs, J.R. & N.B. Davies. 1993. An Introduction to Behavioral Ecology. 3rd ed. Blackwell Scientific Publications, Oxford. 482pp.

Levi, H.W. 1948. Notes on the life history of the pseudoscorpion *Chelifer cancroides* (Linn.) (Chelonethida). Transactions of the American Microscopical Society 67:290–290.

Levi, H.W. 1953. Observations on two species of pseudoscorpions. Canadian Entomologist 85:55–62.

Oliveira, P.S & R.J. Marquis. 2002. The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna. Columbia University Press, New York. 398pp.

Martin, P. & P. Bateson. 1993. Measuring Behaviour: An Introductory Guide. 2nd ed. Cambridge University Press, Cambridge. 222pp.

Plateaux-Quénu, A., A. Horel & C. Roland. 1997. A reflection on social evolution in two different groups of arthropods: halictines bees (Hymenoptera) and spiders (Arachnida). Ethology Ecology & Evolution: 9:183–196.

Weygoldt, P. 1969. The Biology of Pseudoscorpions. Harvard University Press, Cambridge. 145pp.

Wilson, E.O. 1971. The Insect Societies. Harvard University Press, Cambridge. 548pp.

Zeh, D.W. 1987. Aggression, density and sexual dimorphism in chernetid pseudoscorpions (Arachnida: Pseudoscorpionida). Evolution 41(5):1072–1087.

Zeh. J.A. & D.W. Zeh. 1990. Cooperative foraging for large prey by *Paratemnus elongatus* (Pseudoscorpionida, Atemnidae). Journal of Arachnmology 18:307–311.

Zeh. J.A. & D.W. Zeh. 2001. Spontaneous abortion depresses female sexual receptivity in a viviparous arthropod. Animal Behaviour 62:427–433.

Manuscript received 15 September 2003, revised 20 February 2004.

2005. The Journal of Arachnology 33:878–879

BOOK REVIEW

Review of Fossil Spiders in Amber and Copal by Joerg Wunderlich. Published by the author (Verlag J. Wunderlich) in two volumes under the reference Beiträge zur Araneologie 3a (Volume 1 with 848 pages) and 3b (Volume 2 with 1060 pages). ISBN 3-931473-10-4. Cost for each volume is 48 Euro with orders to be placed with the author at Ober Häuselbergweg 24, Hirschberg, 69493, Leutershausen, Germany.

This voluminous work covers every conceivable aspect of fossil spiders in amber and copal, from systematics and evolution to behavior and ecology. Since our conceptions of fossils are based on our knowledge of extant forms, many examples of modern day taxa are used to interpret the behavior of fossil taxa (Boucot 1990). The present work differs from the authors two earlier books on fossil spiders (Spinnenfauna gestern und heute [1986] and Die fossilen Spinnen im Dominikanischen Bernstein [1988]) by being written in both English and German, thus making it accessible to a wider audience.

Reviewing a book of 1908 pages is no small task and I apologize if some aspects, which have special significance to certain readers, are omitted. Since pagination continues sequentially in both volumes, I will refer to the two as a single work. To begin, this definitely is a "one of a kind book" which has its own unique type of presentation. Most of the chapters appear as separate publications with a title, author, abstract, introduction, references and figures, so they can be cited separately. Some of the final chapters are authored by others.

This book presents a wealth of information on all aspects of fossil spiders in amber and copal, although most of the new taxa and examples presented are in Baltic and Dominican amber and Madagascar copal. While the major part of the book covers systematic placement and taxonomic descriptions of fossil spiders, a large and significant section deals with fossil evidence of spider biology and behavior. Topics in this portion include leg amputation and regeneration, ballooning, bleeding, camouflage, webs, sperm and sperm webs, courtship behavior, egg sacs, enemies, fecal remains, exuviae, ant mimicry, wound healing, molting, cannibalism, parasitism, phoresis and predation by spiders on a wide range of other organisms (including beetles, flies, bark lice, ants, planthoppers, termites, other spiders, caddis flies, parasitic wasps, scale insects, spring tails, roaches, aphids, mites, a web spinner, weevils, bristle tails, insect larvae, myriapods and pseudoscorpions).

Of special interest are the author's comparisons of extant and extinct spiders in Europe and the Dominican Republic based on present day records and amber taxa. While amber only entraps a small percentage of spiders in any ecosystem, it is amazing how many species have been found. In Dominican amber, there are some 152 spider species in comparison with 296 extant ones in the Dominican Republic while Baltic amber has some 500 species in comparison with some 1300 extant ones in Northern Europe. At the higher level, there are more spider families in Baltic amber (51) than in Europe today (46).

Findings show that Theridiidae is the dominant family in both Baltic and Dominican amber, thus reflecting the tropical-subtropical conditions at both of those sites in the mid-Tertiary. In contrast, the Linyphiidae is the most diverse family in central Europe today, reflecting the temperate climate. Spiders in Baltic amber are over twice as diverse as in Dominican amber. This is probably due to the

different ecotypes in the Baltic amber forest, including not only subtropical-tropical, but also warm temperate forms (Larsson 1978). This diversity is also reflected in the plant genera reported from Baltic amber. The tropical-subtropical and many warm temperate forms undoubtedly disappeared during the post-Eocene cooling events (Prothero 1994). In contrast, the climate in Hispaniola remained fairly constant until the Pliocene-Pleistocene cooling period, which eliminated the strictly tropical forms (Poinar & Poinar 1999). This explains why approximately 88% of the spider taxa in Baltic amber are now extinct, compared with only 33% in Dominican amber.

Since fossilized resin is the best medium for preserving taxonomic characters, a wealth of new fossil taxa have been described from specimens preserved in amber and copal. A number of new spider species and genera are described in the present work, mostly from Baltic and Dominican amber, but a few also in Lebanese and Burmese amber. Each chapter in volume 2 deals with a specific spider family, usually beginning with a key to the amber species and then describing new taxa.

Of all the spiders covered in this work, one group in particular is especially interesting because of its phylogeny, appearance and biogeography. These spiders belong to the primitive family Archaeidae, the "Dawn" or "Long- necked spiders". Wunderlich lists two subfamilies, the Mecysmaucheniinae, from Australia, New Zealand and South America and the Archaeinae from South Africa, Madagascar and the Australian Region. Five genera in the subfamily Archaeinae occur in Baltic and Bitterfeld amber, the most common fossil being *Archaea paradoxa* Koch & Berendt 1854 in Baltic amber. Members of the genus *Archaea* have an elongated prosoma and long chelicerae, the inner edges of which are lined with peg teeth to grasp prey. All extant members of this subfamily prey on spiders and the long chelicerae hold the prey far enough away to avoid receiving injury. Dawn spiders are quite small (usually less than 4 mm in length); do not make capture nets, live among dead leaves or moss and lichens on tree limbs and carry around their egg sacs. Wunderlich shows an *Arachaea* sp. in Baltic amber holding a member of the family Theridiidae as prey. The descendants of *Archaea* are long gone from the Northern Hemisphere but can be found in Madagascar copal, a product of the legume tree, *Hymenaea verrucosa*. Today, most copal from Madagascar is less than 100 years old, yet at the rate of habitat destruction in that land, it is an important source of rare and endangered and probably even extinct species (Poinar et al 2001).

Volume one contains 696 color photos of spiders covered in the text and numerous examples of spider behavior. Also included are color photos of the only known Baltic amber solfugid and opilioacarid. The unique type of presentation and some spelling errors in this work should not detract from its wealth of information, which will be of interest not only to arachnologists, but amber enthusiasts in general, since the color plates are quite fascinating and the keys can be used for the identification of amber and copal spiders.

LITERATURE CITED

Boucot, A. 1990. Evolutionary Paleobiology of Behavior and Coevolution. Elsevier, Amsterdam. 725 pp.

Larsson, S.G. 1978. Baltic Amber—a Palaeobiological Study. Entomonograph 1:1–192.

Poinar, Jr., G.O., A. Brown, S. Brown & R. Poinar. 2001. Stuck in Time (Madagascar copal). Fauna 2:70–76.

Poinar, Jr., G.O. & R. Poinar. 1999. The Amber forest. Princeton University Press, Princeton. 239 pp.

Prothero, D.R. 1994. The Eocene-Oligocene Transition. Columbia University Press, New York. 291 pp.

Wunderlich, J. 1986. Spinnenfauna gestern und heute. Erich Bauer Verlag, Wiesbaden. 283 pp.

Wunderlich, J. 1988. Die fossilen Spinnen (Araneae) im Baltischen Bernstein. Beiträge zur Araneologie 3:280 pp.

George Poinar, Jr.: Department of Zoology, Oregon State University, Corvallis, OR 97331 Email: poinarg@science.oregonstate.edu

INSTRUCTIONS TO AUTHORS

(revised October 2003)

General: Manuscripts are accepted in English only. Authors whose primary language is not English may consult the editors for assistance in obtaining help with manuscript preparation. All manuscripts should be prepared in general accordance with the current edition of the *Council of Biological Editors Style Manual* unless instructed otherwise below. Authors are advised to consult a recent issue of the *Journal of Arachnology* for additional points of style. Manuscripts longer than three printed journal pages should be prepared as Feature Articles, shorter papers as Short Communications. One invited Review Article per year will be solicited by the editors and published in the third issue at the discretion of the editors. Suggestions for review articles may be sent to the Managing Editor.

Submission: Send one electronic version of the entire manuscript (in PDF or Microsoft Word format) or send four identical copies of the typed material together with copies of illustrations to the Managing Editor of the *Journal of Arachnology*: **Paula E. Cushing, *Managing Editor*, Denver Museum of Nature and Science, Zoology Department, 2001 Colorado Blvd., Denver, CO 80205-5798 USA** [*Telephone:* (303) 370-6442; *FAX:* (303) 331-6492; *E-mail:* PCushing@dmns.org or PECushing@juno.com].

The Managing Editor will forward your manuscript to one of the Subject Editors for the review process. You will receive correspondence acknowledging the receipt of your manuscript from the Managing Editor, with the manuscript number of your manuscript. Please use this number in all correspondence regarding your manuscript. Correspondence relating to manuscripts should be directed to the appropriate Subject Editor. After the manuscript has been accepted, the author will be asked to submit the manuscript on a PC computer disc in a widely-used word processing program. The file also should be saved as a text file. Indicate clearly on the computer disc the word processing program used.

Voucher Specimens: Voucher specimens of species used in scientific research should be deposited in a recognized scientific institution. All type material must be deposited in a recognized collection/institution.

FEATURE ARTICLES

Title page.—The title page will include the complete name, address, and telephone number of the author with whom proofs and correspondence should be exchanged, a FAX number and electronic mail address if available, the title in capital letters, and each author's name and address, and the running head (see below).

Abstract. —The heading in bold and capital letters should be placed at the the beginning of the first paragraph set off by a period. A second abstract, in a language pertinent to the nationality of the author(s) or geographic region(s) emphasized, may be included.

Keywords. — Give 3–5 appropriate keywords following the abstract.

Text. —Double-space text, tables, legends, etc. throughout. Three levels of heads are used.

- The first level (METHODS, RESULTS, etc.) is typed in capitals and on a separate line.
- The second level is **bold,** begins a paragraph with an indent and is separated from the text by a period and a dash.
- The third level may or may not begin a paragraph but is italicized and separated from the text by a colon.

Use only the metric system unless quoting text or referencing collection data. All decimal fractions are indicated by the period (e.g., -0.123).

Citation of references in the text: Cite only papers already published or in press. Include within parentheses the surname of the author followed by the date of publication. A comma separates multiple citations by the same author(s) and a semicolon separates citations by different authors, e.g., (Smith 1970), (Jones 1988; Smith 1993), (Smith 1986, 1987; Smith & Jones 1989; Jones et al. 1990). Include a letter of permission from any person who is cited as providing unpublished data in the form of a personal communication.

Citation of taxa in text: Please include the complete taxonomic citation for each arachnid taxon when it appears first in the paper. For Araneae, this taxonomic information can be found on-line at http://research.amnh.org/entomology/spiders/catalog81-87/INTRO2.html. For example, *Araneus diadematus* Clerck 1757.

Literature cited section.—Use the following style and include the full unabbreviated journal title.

Opell, B.D. 2002. How spider anatomy and thread configuration shape the stickiness of cribellar prey capture threads. Journal of Arachnology 30:10–19.

Krafft, B. 1982. The significance and complexity of communication in spiders. Pp. 15-66. *In* Spider Communications: Mechanisms and Ecological Significance. (P.N. Witt & J.S. Rovner, eds.). Princeton University Press, Princeton, New Jersey.

Footnotes.—Footnotes are permitted only on the first printed page to indicate current address or other information concerning the author. All footnotes are placed together on a separate manuscript page. Tables and figures may not have footnotes.

Running head.—The author's surname(s) and an abbreviated title should be typed all in capital letters and must not exceed 60 characters and spaces. The running head should be placed near the top of the title page.

Taxonomic articles.—Consult a recent taxonomic article in the *Journal of Arachnology* for style or contact the Subject Editor for Systematics. Papers containing the original taxonomic description of the focal arachnid taxon should be given in the Literature Cited section.

Tables.—Each table, with the legend above, should be placed on a separate manuscript page. Only horizontal lines (usually three) should be included. Tables may not have footnotes; instead, include all information in the legend. Make notations in the text margins (if possible) to indicate the preferred location of tables in the printed text. Must be double spaced.

Illustrations.—Original illustrations should not be sent until the article is accepted for publication. Electronic submissions of illustrations is acceptable for review of the manuscript. However, final versions of illustrations of accepted manuscripts must still be submitted in hard copy (camera-ready, instructions below). Address all questions concerning illustrations to the Editor of the *Journal of Arachnology*: **Dan Mott, *Editor-In-Chief*, Department of Biology & Chemistry, Texas A&M International University, 5201 University Blvd., Laredo, TX 78041-1900 USA** [*Telephone* (956) 326-2583; *FAX:* (956) 326-2439; *E-mail:* dmott@tamiu.edu]. All art work must be camera-ready — i.e., mounted and labeled — for reproduction. Figures should be arranged so that they fit (vertically and horizontally) the printed journal page, either one column or two columns, with a minimum of wasted space. When reductions are to be made by the printer, pay particular attention to width of lines and size of lettering in line drawings. Multiple photos assembled on a single plate should be mounted with only a minimum of space separating them. In the case of multiple illustrations mounted together, each illustration must be numbered sequentially rather than given an alphabetic sequence. Written on the back should be the name(s) of author(s) and an indication of top edge. Indicate whether the illustration should be one column or two columns in width. The overall dimensions should be no more than 11 inches (28 cm) x 14 inches (36 cm). Larger drawings present greater difficulty in shipping and greater risks of damage for which the *Journal of Arachnology* assumes no responsibility. In manuscripts for review, photocopies should be included, and should be reduced to the exact measurements that the author wants to appear in the final publication. Make notations in the text margins to indicate the preferred position of illustrations in the printed text. Color plates can be printed, but the author must assume the full cost, currently about $600 per color plate.

Legends for illustrations should be placed together on the same page(s) and separate from the illustrations. Each plate must have only one legend, as indicated below:

Figures 1-4.— *A-us x-us*, male from Timbuktu: 1. Left leg; 2. Right chelicera; 3. Dorsal aspect of genitalia; 4. Ventral aspect of abdomen.

Figures 27-34.—Right chelicerae of species of *A-us* from Timbuktu: 27, 29, 31, 33. Dorsal views; 28, 30, 32, 34. Prolateral views of moveable finger; 27, 28. *A-us x-us*, holotype male; 33, 34. *A-us y-us*, male. Scale = 1.0 mm.

Assemble manuscript for mailing.—Assemble the separate sections or pages in the following sequence; title page, abstract, text, footnotes, tables with legends, figure legends, figures.

Page charges, proofs and reprints.—Page charges are voluntary, but non-members of AAS are strongly encouraged to pay in full or in part for their article ($75/journal page). The author will be charged for changes made in the proof pages. Reprints are available only from the Allen Press and should be ordered when the author receives the proof pages. Allen Press will not accept reprint orders after the paper is published. The *Journal of Arachnology* also is published by BioOne. Therefore, you can download the PDF version of your article from the BioOne site or the AAS site if you are a member of AAS or if your institute is a member of BioOne. PDF's of articles older than one year will be freely available from the AAS website.

SHORT COMMUNICATIONS

Short Communications are usually limited in length to three journal pages, including tables and figures. They will be printed in a smaller (10 point) typeface. The format for these is less constrained than for feature articles: the text must still have a logical flow, but formal headings are omitted and other deviations from standard article format can be permitted when warranted by the material being covered.

Short Communications

Book Review

USERNAME: akron05 PASSWORD: spider05

CONTENTS

The Journal of Arachnology

Volume 33 Featured Articles Number 3

Review Article

Contents continued on inside back cover